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RECENT DEVELOPMENTS IN FISHERY SCIENCE IN JAPAN AND ASIA

John J. Magnuson*

Approximately 40 per cent of the world's catch of fish is made by Asian countries, notably Japan, Russia, and mainland China. Numerous developing countries in Asia are eager to expand and improve their harvest. Research appears to have the broad aims of developing new fisheries, managing existing fisheries effectively, and improving fish-culture techniques. Recent developments were presented at several symposia at the 11th Pacific Science Congress in Tokyo, 1966, on subjects as diverse as the high seas tuna resources and culture of algae. More comprehensive summaries of developments were presented at the 12th Session of the Indo-Pacific Fisheries Council in Honolulu, 1966. An additional Symposium on Tuna Fisheries was held in Tokyo in 1966 and was summarized in the *Bulletin of the Japanese Society of Scientific Fisheries*, volume 32, number 9.

Developments have occurred in the research on many fisheries but because of our position in the central Pacific, those in Japan's high seas tuna fisheries are perhaps of most interest to Hawaiians. The Nankai Regional Fisheries Research Laboratory, responsible for this research, has been studying tuna biology, stock assessment, and tuna oceanography since 1950. The research depends largely upon the fishery as a source of data. During the early growth of the tuna longline fishery, the resource was considered to be practically inexhaustible. From 1952 to 1962 longline fishing spread to all the oceans of the world and increased fivefold. In their stock-assessment studies Japanese scientists have recently noted that some tuna stocks appear to have been fished at equilibrium levels since the early 1960's. In some areas additional fishing effort would not be expected to increase the yields. A new high seas laboratory, being established in Shimizu City, will combine all research activities on Japan's distant-water fisheries. The work will include research on tuna, salmon, distant-water trawling, whales, and fur seals.

Research to improve the efficiency of fishing gear so as to reduce manpower requirements is receiving new impetus in many areas of Japan, because it has become increasingly difficult to recruit young men to a sea-going life. Present activities include attempts to mechanize both longline and pole-and-line fishing, and also to improve accuracy in selecting the depth at which longline hooks are fished.

Fish culture, important in Asia, is certainly not new. Common carp (*Cyprinus carpio*) was economically important in China 2,400 years ago. Today in Japan the most important species cultured are eel (*Anguilla japonica*), yellowtail (*Seriola quinquiradiata*), common carp, rainbow trout (*Salmo gardneri irideus*), alga laver (*Porphyra tenera*), oyster (*Ostrea gigas*), and pearl oyster (*Pinctada martensis*). In 1964 these and other cultured species made up 7 per cent of the total Japanese output. In mainland China about 40 per cent of the total catch is from fresh water. Apparently most of this catch is cultured. A major development in fish culture has been the perfection of techniques to induce spawning artificially by injecting pituitary hormones. It is expected that this recent development will ensure a large and regular supply of fish fry for culture. Progress in inducing spawning was realized in at least four different countries with at least eight species from fresh and brackish water culture. Another advance is the increase in cultivation of shrimp and other invertebrates.

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Flume Experiments on the Hydrodynamics of Plankton Nets

By

C. V. W. Mahnken

and

J. W. Jossi

Flume Experiments on the Hydrodynamics of Plankton Nets[1]

By

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Experiments on the dynamics of flow into conical plankton nets were conducted at the US Navy's David Taylor Model Basin. A pitot tube and a telemetering flowmeter were used to measure the distribution of flow across the mouths of three 1 m diameter nets with mesh apertures of 0.281 mm, 0.221 mm, and 0.111 mm. Velocity profiles at the mouth of bridled nets consistently showed maximum velocity near the margin of the mouth, and a distinct minimum at the centre. The velocity was uniform across the mouth of an unbridled net that was tested. The filtration efficiency of all nets was high at normal towing speeds and remained high up to speeds of 257 cm/sec. Sustained high efficiencies were due in part to stretching of the nylon material from which the nets were constructed.

Introduction

The necessity for quantitative measurements of the zooplankton community is well known, but flowmeter data from most commonly used samplers are difficult to interpret because of inability to determine the absolute volume of water filtered. Information on filtering efficiency and flow patterns derived from controlled flume experiments is necessary to establish the significance of flowmeter readings, and to suggest principles for the future design of plankton samplers.

Experiments to measure selected flow characteristics of conical plankton nets were conducted in the Circulating Water Channel at the US Navy's David Taylor Model Basin in October 1964 and April 1965. The objectives were to determine: (1) the relation between the total volume of water entering a plankton net and the volume measured by a meter mounted in the mouth of the net; and (2) how the filtering efficiency varied with changes in towing speed and mesh size.

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[1] Contribution No. 26, US Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida.

| J. Cons. perm. int. Explor. Mer | 31 | No. 1 | 38–45 | Copenhague, Avril 1967 |

Table 1

Dimensions of three numbers of "Nitex" netting. Numbers 280 and 223 have single-strand, woven mesh. Number 110 has single strands in one direction, but alternating single and double strands in the other direction

		Mesh Aperture sizes (mm)				Thread sizes (mm)			
Nitex No.	Number of measurements	Min.	Mean	Max.	Number of measurements	Single weft	Single warp	Double warp	Percentage open area
280	250	0·256	0·281	0·306	50	0·171	0·171	–	39
223	100	0·188	0·221	0·244	100	0·122	0·122	–	42
110	100	0·094	0·111	0·125	50	0·045	0·057	0·088	43

Materials and Methods

Three plankton nets with the same dimensions, but different mesh sizes, were tested in the flume. Included was the ICITA net, used by all participants in the International Cooperative Investigations of the Tropical Atlantic (Austin, 1963), and in continued use by the Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida. To date, more than 1400 plankton samples have been collected with the ICITA net in regions of the tropical Atlantic Ocean.

The nets were conical and consisted of four longitudinal panels. Each net was 364 cm long, 100 cm in mouth diameter, and 10 cm in cod-end diameter. The mouth opening was laced to a brass ring fitted with a 3-wire towing bridle. The three wires of the towing bridle met at a common point 100 cm ahead of the mouth. The flowmeter normally mounted in the mouth of the ICITA net during field work was removed during the experiments. The filtering material of the ICITA net was Nitex[1] brand nylon, No. 280; the other two nets were constructed of Nitex Nos. 223 and 110 (see Table 1 for details). Disregarding the non-filtering portions of the three nets, the ratios of total area of netting aperture to mouth area were 3·09, 2·87, and 3·17, respectively.

The Circulating Water Channel is a straight flume about 15 m long and 7 m wide, with a 2·7 m water depth. Pumps at the downstream end continuously remove water and return it to the upstream end via a conduit beneath the channel. Water velocity in the channel can be controlled through a range of 51–488 cm/sec (1–9·5 knots), with a maximum variation of ± 3·5 cm/sec. Channel velocity was monitored continuously by a pitot tube permanently mounted in the middle of the channel, 1 m off the bottom.

During the October tests, the nets were rigged in the flume as they would be towed in the field, with a 3-wire towing bridle preceding the net mouth. In the April tests, the bridle was replaced with three diverging wires connecting the net ring to the channel walls and bottom. Flow of water was thus unobstructed forward of the net mouth.

In October the field of water velocity in and around the three nets was measured with a Prandtl-type pitot tube of 0·3 cm outside diameter. Fluid with a density of 2·94 g/ml was used in the manometer. Measurements were made at a series of points across the mouth diameters and inside the three nets at channel velocities of 51, 103, 154, 206, and 257 cm/sec (1–5 knots). Early tests indicated

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[1] "Nitex" Tobler, Ernst and Traber, Inc., 71 Murray Street, New York, N.Y. 10007. (Trade names referred to in this manuscript do not imply endorsement of commercial products.)

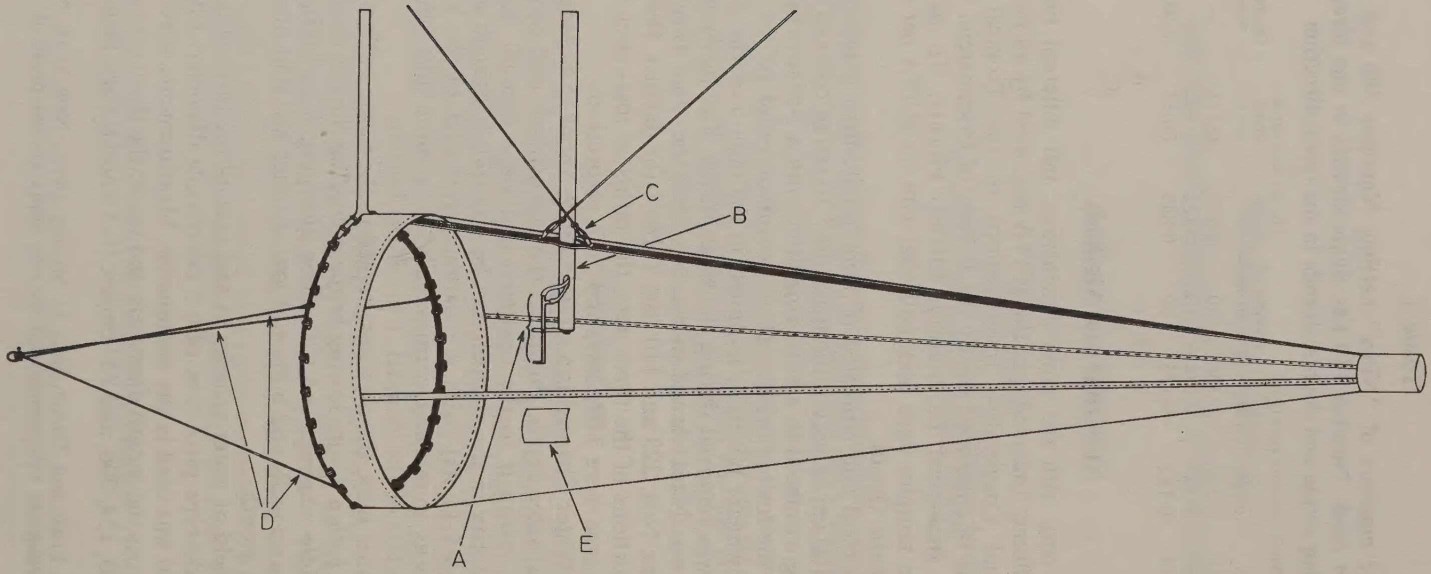

Figure 1. Method of measuring water velocity in a conical plankton net under flow conditions in the David Taylor Model Basin Circulating Water Channel. A) pitot tube B) instrument strut C) double-tabbed zipper D) towing bridle E) portion of net photographed to determine stretching.

that flow was symmetrical about the centre of the net mouth; consequently, subsequent measurements were made only along the radius from the centre to the bottom edge of the net. In April only the ICITA net was tested. Velocity measurements on the ICITA net mouth and forward of the net were made with two instruments, a pitot tube of 0·6 cm outside diameter, with a 1·75 g/ml density manometer fluid, and a telemetering Marine Advisors[1] flowmeter. The impeller housing of the flowmeter is 7·6 cm in diameter and 15·2 cm long. Electrical impulses, caused by magnets in the five rotating fibre-glass impeller blades, are telemetered to the surface via an electrical cable. Both the pitot tube and the flowmeter could be mounted on the lower end of a strut for positioning in and around the nets. A racking device for the strut provided precise vertical and horizontal positioning of the instruments at all channel velocities. Channel velocities were the same as those used in October.

Velocity measurements inside the net were made by inserting the instruments through a double-tabbed zipper extending from the mouth to the cod-end along the uppermost longitudinal seam of the net (Figure 1). Results of the internal measurements are not reported in the present paper.

Telephotographs of the No. 110 Nitex net under flow conditions were taken through a window in the Circulating Water Channel at velocities of 31, 62, 124, 185, and 247 cm/sec. A millimetre rule was sewed loosely on the portion of the net to be photographed to provide an absolute scale for measurement. The number of apertures was counted in a 15 × 15 mm area of mesh in each photograph.

Results

Measurements of the three bridled nets revealed non-uniform flow across the mouth openings. Velocities were maximum near the peripheries and minimum at the centres (Figure 2-A). Flow near the peripheries actually exceeded channel velocity in some observations. The difference between peripheral and central velocities increased with channel velocity. Measurements of the unbridled ICITA net showed uniform velocity across the mouth (Figure 2-B).

Filtering efficiency was determined by comparing the experimentally measured flux of water through the mouth of each net with the flux through a netless ring. The filtering efficiency of the No. 280 Nitex net at 51 cm/sec, as measured the October experiments, was somewhat lower than the value obtained in April (Figure 3). Slow response of the manometer fluid due to the small diameter of the pitot tube used in October is believed to be responsible for these low readings. Subsequent flume tests by the Bureau of Commercial Fisheries and the National Academy of Sciences yielded data which substantiated the higher flowmeter efficiencies. At 103 cm/sec, the efficiencies of the three nets were greater than 97 per cent. The efficiency of the ICITA net in October decreased above 103 cm/sec, but leveled off between 206 and 257 cm/sec. The April data for the ICITA net and the October data for the Nos. 223 and 110 nets showed that the efficiencies did not consistently decrease with increased channel velocity above 103 cm/sec, but tended to level off or even rise above that point. Filtering efficiencies of the unbridled ICITA net were not significantly lower than those of the bridled net. The high filtering efficiencies of the

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[1] Marine Advisors, Inc., P. O. Box 1963, 7440 Girard Ave., La Jolla, California 92038.

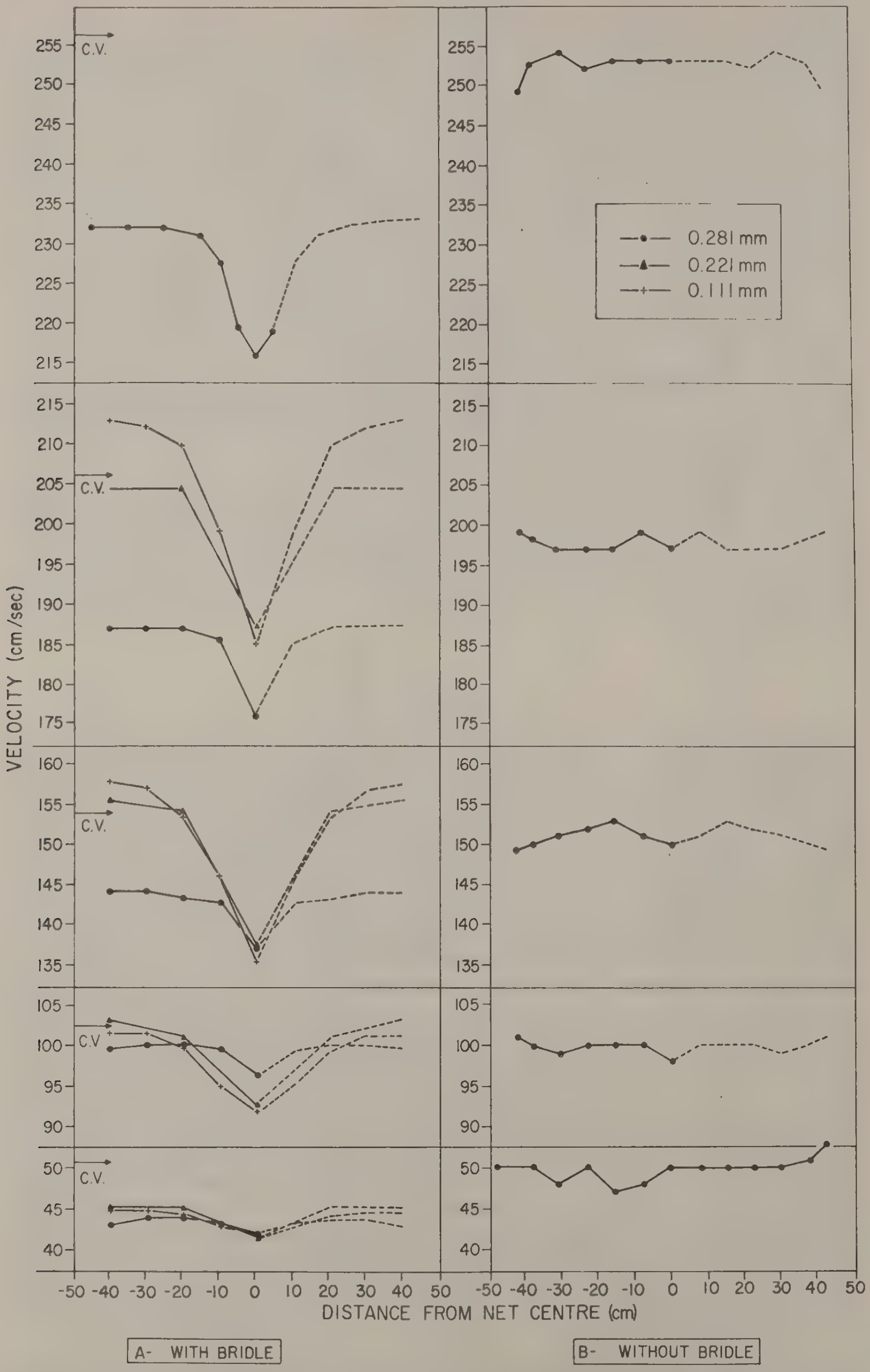

Figure 2. Velocity profiles in the mouths of three conical plankton nets at different channel velocities (C. V.), (A) with towing bridle and (B) without towing bridle. Symbols in the upper right panel indicate mesh sizes of the nets. The solid lines show velocities measured along the radius of the mouth of the net; broken lines are mirror images of the solid lines.

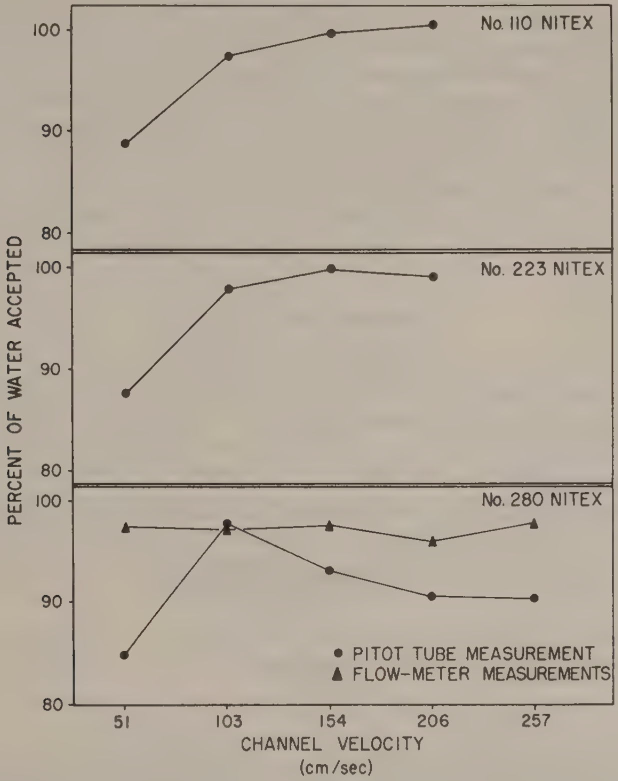

Figure 3. Filtering efficiencies for three conical plankton nets of different mesh sizes at different channel velocities.

nets at the higher channel velocities may have resulted from stretching of the mesh material.

Figure 4 illustrates the change in the number of mesh apertures in a 15 × 15 mm area of netting as channel velocity increased. The greatest amount of stretching occurred between 103 and 206 cm/sec, but the material continued to stretch up to speeds of 247 cm/sec, the highest speed at which photographs were made. The amount of stretching indicated in Figure 4 cannot be used to quantify the change in filtering efficiency, because it represents only one spot on the net, approximately 1 m from the mouth.

Discussion

The effect of the bridle on flow distribution can be demonstrated by comparing the velocity profiles of the bridled nets with those of the unbridled net. The net without a bridle had a relatively uniform distribution of velocity across the net mouth at all channel velocities tested. The non-uniform distribution of flow of the bridled nets is attributed to the presence of the towing bridle.

The velocity profiles provide a basis for determining the optimum location

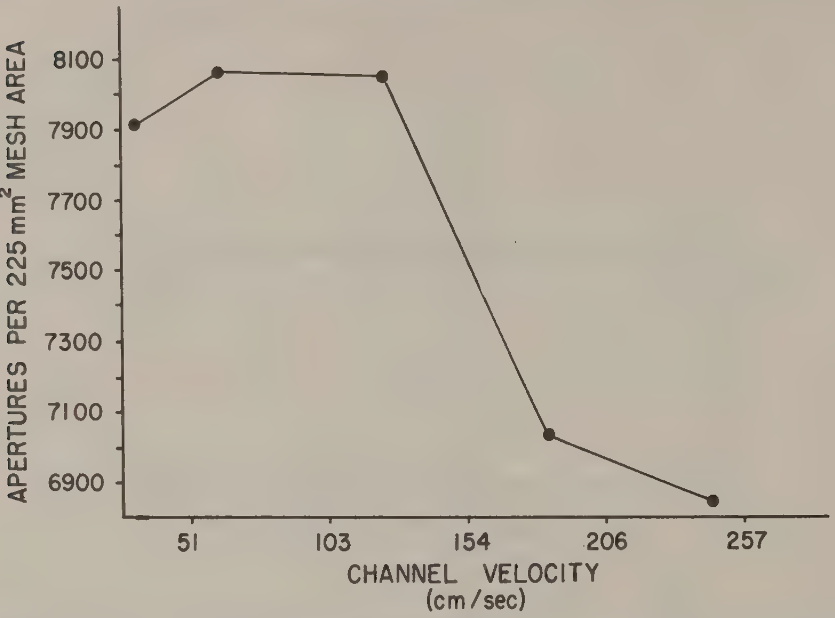

Figure 4. Changes in the number of mesh apertures per 15 × 15 mm area of netting with increasing channel velocity. A decrease in aperture count indicates stretching of the net material.

of a meter in the mouths of bridled nets to monitor flow most accurately. A meter mounted in the low-velocity central core would give low values for the total volume of water entering the net. Correction factors would have to be applied to readings of a central meter to determine the amount of water filtered by the net. The flow at a distance of 25–40 cm from the centre is more representative of mean flow through the entire mouth, and the range of velocity between these two points is small. A meter mounted in this relatively steady velocity "plateau" would give more accurate values for the total volume of water entering the net.

Nishizawa and Anraku (1956) conducted field tests on a similar conical plankton net with flowmeters mounted centrally and peripherally. They found that the velocity at the centre of the mouth was always 20–30 per cent lower than at the periphery at hauling speeds of 90–130 cm/sec. This difference is roughly equivalent to the 6–36 per cent difference observed by us in similar field tests. An alternative solution to an off-centre mounting of the flowmeter would be to eliminate the bridle completely, as described by Nakae (1962), thus removing the source of discontinuous flow. Elimination of the bridle would not only solve the problem of meter placement, but would negate any effect the bridle might have of forewarning organisms of the approach of the net.

All three nets changed shape with varying channel velocities. At low velocities, the net assumed the shape of a cone preceded by a loose, billowy, cylindrical section, approximately 1 m long. As channel velocities increased from 51 to 154 cm/sec, the length of the cylindrical section decreased, and above 154 cm/sec, the net assumed precisely the configuration of a cone. We believe that the point of inflection between cylinder and cone represents the boundary between netting of low filtering rate in the cylindrical section and high filtrating rate in the conical section. It is reasonable to suppose that a channel velocity exists beyond which a net can no longer filter all the water encountered. When maximum capacity is reached, all other variables remaining constant, it follows that a further increase in channel velocity would result in a rejection of water and a decrease in filtering efficiency. In the present study, either this maximum capacity was not reached or some other variable (e.g., stretching of the Nitex material) acted to sustain the filtering efficiency.

Acknowledgements

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Summary

A discontinuity in flow across the mouths of three conical, bridled plankton nets was observed when the nets were tested in a circulating water channel. Maximum flow occurred at the periphery and a distinct minimum occurred at the centre of the nets. The discontinuity was due to interference by the towing bridles. Effect of this discontinuity were:

(1) To reduce the amount of water passing through a centrally-mounted flowmeter as compared with the mean amount passing through the entire mouth. Low estimates for the volume of water filtered would be obtained from these meter readings.

(2) To reduce slightly the filtration efficiency of the net.

(3) Possibly, to forewarn organisms of the approaching net. It is recommended that the flowmeter be mounted in an off-centre position, or that the bridle be eliminated.

Filtration efficiencies of the three nets were high at all channel velocities tested; and are explained in part by the stretching of the material from which the nets were constructed.

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Diatoms as Food of Larval Sea Lampreys in a Small Tributary of Northern Lake Michigan

PATRICK J. MANION

Diatoms as Food of Larval Sea Lampreys in a Small Tributary of Northern Lake Michigan

INTRODUCTION

The food and food preferences of sea lamprey ammocoetes have not been investigated. The food of the larval American brook lamprey, *Lampetra lamottei* (Lesueur) (*Entosphenus appendix* of the authors), in the Great Lakes region consisted mainly of diatoms and desmids according to Creaser and Hann (1929). Schroll (1959) discussed the biology of feeding of ammocoetes of *Lampetra planeri* (Bloch) and *Eudontomyzon danfordi* (Regan) in Europe. This report presents data on the availability and use of diatoms by sea lamprey, *Petromyzon marinus*

Linnaeus, ammocetes in a small tributary of northern Lake Michigan.

MATERIALS AND METHODS

Samples of lamprey ammocoete and diatoms were collected on 19 May 1964, from a pool in Snyder-Deadhorse Creek, Schoolcraft County, Michigan. The larvae were collected with an electric shocker and preserved in 5% formalin. The samples consisted of 10 small specimens (33 to 35 mm long, about 2 years old) and 10 large larvae (70 to 72 mm long, about 4 years old). Preliminary examination indicated that ammocoetes within each of the two size groups contained comparable numbers and species of diatoms. Schroll (1959) also found that ammocetes of comparable ages in several rivers of Europe consumed similar numbers of various diatoms. Therefore, the 10 ammocoetes in each size group were treated as a unit.

Diatoms were recovered from the intestine of small ammocoetes by dissolving the 10 larvae in a concentrated nitric acid-potassium dichromate bath, leaving the diatoms in solution. Only the intestines of the 10 large ammocetes were digested in the acid bath; this eliminated excessive fat droplets that hinder the preparation of slides and interfere with diatom counts.

Diatoms in the stream were sampled by collecting 1-liter water samples at the location where the ammocetes were taken. Water depth was 18 inches; samples were taken at the surface, middepth, and bottom. After the water was filtered through Millipore paper (pore size 0.45 ± 0.02 micron), the diatoms were removed by dissolving the paper in a nitric acid-potassium dichromate solution.

Each sample of ammocoetes and water was deacidified and concentrated to a 3-ml stock solution by repeated washing, decantation, and evaporation. Slides were prepared for each sample by the following method: 0.1 ml of the stock solution was spread evenly on a coverslip (No. 0, 18 mm square), allowed to dry, then heated at 200 C for ½ hour to remove all water; the coverslip was then inverted and placed on a drop of Hyrax mounting medium (refractive index 1.65) on a slide; and the slide was heated at 200 C until all the gases were released from the Hyrax. Three slides were prepared for each sample, of which two were selected for the counts.

Identification and counts were made at a magnification of 970×. Counts with an ocular micrometer included 126 mm^2 of each slide. Numbers of diatoms on the two slides from each sample were not significantly different.

AVAILABILITY AND UTILIZATION OF DIATOMS

Water samples and 20 ammocoete samples contained 17 genera of diatoms (total for all samples, 21—see Table 1). *Synedra, Fragilaria, Navicula, Gomphonema, Meridion*, and *Cocconeis* constituted approximately 98% of the diatoms in the water and 97% of the diatoms eaten by the ammocoetes. The percentage composition for various genera was similar for the three strata of water, but the number of diatoms was greatest near the bottom and least at the surface. The counting technique did not distinguish between live and dead diatoms; I do not know whether shells of dead diatoms contributed to the larger number on the bottom.

The abundant genera occurred at frequencies that were significantly different (as determined by a chi-square test; $P = 0.001$, $df = 6$) in the water and the two size groups of ammocoetes (Table 1). *Synedra* was most abundant in the water samples (40.3–45.4%) and in small ammocoetes (46.6%), but accounted for only 22.2% of the diatoms consumed by large ammocoetes. *Fragilaria* was less well represented in both groups of larvae than in the water. It constituted only 8.7% of the diatoms in the small ammocoetes and 14.4% in the large ammocoetes, as compared with 24.3–31.7% in the stream.

Navicula made up only 7.7–11.5% of the diatoms in the stream (the lowest concentration was at the bottom where the larvae were feeding), but constituted 32.9% of the diatoms taken by large ammocoetes and 19.1% of those eaten by small larvae. *Gomphonema* occurred in the same concentrations on the bottom (7.7%) as *Navicula*; it was less well represented in larvae of both size groups (11.9–13.0%) than *Navicula*, but like *Navicula* was better represented in the larvae than in the

TABLE 1.—*Percentage composition of various genera of diatoms in samples of water and in sea lamprey ammocetes from Snyder–Deadhorse Creek, Michigan. Number of individuals in parentheses. T is trace < .05%*

Genus	Water[1]			Ammocoetes	
	Surface	Mid-depth	Bottom	33–35 mm	70–72 mm
Synedra	42.2 (277)	45.4 (439)	40.3 (888)	46.6 (533)	22.2 (595)
Fragilaria	26.0 (171)	24.3 (235)	31.7 (699)	8.7 (99)	14.4 (385)
Navicula	10.8 (71)	11.5 (111)	7.7 (170)	19.1 (218)	32.9 (881)
Gomphonema	6.1 (40)	6.1 (59)	7.7 (170)	11.9 (136)	13.0 (347)
Meridion	9.4 (62)	7.7 (74)	6.5 (142)	7.1 (81)	8.2 (220)
Cocconeis	3.7 (24)	3.7 (36)	4.2 (92)	3.7 (42)	6.0 (160)
Cymbella	0.9 (6)	0.6 (6)	0.3 (6)	1.1 (13)	1.3 (35)
Amphora	0.2 (1)	0.3 (3)	0.7 (16)	0.3 (3)	0.2 (4)
Achnanthes	0.0	0.0	0.3 (7)	0.0	0.4 (11)
Tabellaria	0.0	0.0	0.2 (4)	0.2 (2)	T (1)
Surirella	0.2 (1)	0.2 (2)	T (1)	0.3 (3)	0.1 (3)
Eunotia	0.3 (2)	0.0	0.1 (2)	0.1 (1)	0.1 (3)
Diploneis	0.0	0.1 (1)	0.1 (2)	0.3 (3)	0.3 (7)
Diatoma	0.0	0.0	T (1)	0.0	0.0
Pinnularia	0.0	0.1 (1)	T (1)	0.1 (1)	0.5 (12)
Amphipleura	0.3 (2)	0.0	T (1)	0.0	T (1)
Stauroneis	0.0	0.0	T (1)	0.2 (2)	0.1 (3)
Cyclotella	0.0	0.0	0.0	0.3 (3)	T (1)
Neidium	0.0	0.0	0.0	0.3 (3)	T (1)
Hantzschia	0.0	0.0	0.0	0.0	0.2 (4)
Rhopalodia	0.0	0.0	0.0	0.0	0.2 (5)
Total	100.0 (657)	100.0 (967)	100.0 (2,203)	100.0 (1,143)	100.0 (2,679)

[1] Stream depth at the sampling location was 18 inches.

stream. *Meridion* was similarly represented in the stream (6.5–9.4%) and ammocoetes (7.1–8.2%). The percentage occurrence of *Cocconeis* was similar in the water (3.6–4.2%) and in small ammocoetes (3.7%), but was slightly greater in the large ammocoetes (6.0%).

FEEDING SELECTIVITY

Schroll (1959) has demonstrated that the use of diatoms by larval lampreys is influenced by availability of the diatoms, and by preference of the ammocoetes and the selectivity of their feeding apparatus.

In Snyder-Deadhorse Creek, selection favored *Navicula* and *Gomphonema*, which were present in about equal numbers in the water near the bottom, but were approximately 2–4 times more frequent in the food of large ammocoetes, and about twice as frequent in small larvae. *Gomphonema* is attached to the bottom by branched gelatinous stalks, which may make frustules, that break free, more available to ammocoetes which feed by straining the water at or very close to the bottom. *Navicula* is a solitary, free-floating diatom; the reason for the much higher percentages in the larvae than in the water is unknown.

As age or size of the larvae increased, the frequency of occurrence of *Synedra* decreased and that of *Fragilaria* and *Navicula* increased. Since the water and larvae were collected from the same area, these diatoms were presumably equally available to ammocoetes of both size groups.

The characteristics of the sieve apparatus of the ammocoete and the morphology of the different diatom genera may influence the selection of diatoms. The oral sieve, just anterior to the pharynx, blocks larger particles and lets microorganisms and small particles pass. Food particles agglutinate on a mucous band secreted by the branchial glands posterior to the sieve and are passed by cilia toward the intestine. The sieve may block the ribbon-like colonies of *Fragilaria*, which were much less common in the food than in the environment, but apparently did not block the broad, wedge-shaped colonies of *Meridion*.

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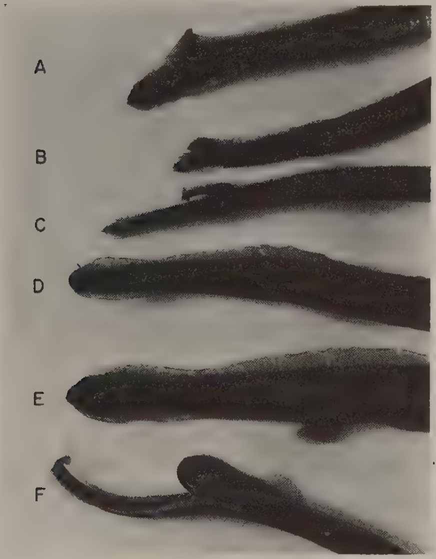

Fig. 1. Lamprey ammocetes with two tails. A–E are sea lampreys, F is an American brook lamprey. Total lengths are: A—120 mm, B—57 mm, C—69 mm, D—113 mm, E—122 mm, F—84 mm.

MORPHOLOGICAL ABNORMALITIES AMONG LAMPREYS.—The experimental control of the sea lamprey (*Petromyzon marinus*) in the Great Lakes has required the collection of thousands of lampreys. Representatives of each life stage of the four species of the Lake Superior basin were examined for structural abnormalities.

The most common aberration was the presence of additional tails (Fig. 1). Among ammocetes that ranged from 10–196 mm, supernumerary tails were present in 10 of 8437 sea lampreys, one of 2726 American brook lampreys (*Lampetra lamottei*) and none of a mixed sample of 635 silver lampreys (*Ichthyomyzon unicuspis*) and northern brook lampreys (*Ichthyomyzon fossor*), which are difficult to separate with certainty. The length of ammocetes with additional tails ranged from 25–122 mm. The extra tails appeared as only buds or bumps on small ammocetes, but were larger and readily distinguishable on larger specimens. The longest accessory tail was 15 mm. Of 3004 recently metamorphosed sea lampreys (range 114–189 mm), one (123 mm) had three caudal fins two of which were abnormal (Fig. 2). Barfurth (1899) found a *Petromyzon planeri* larva with three tails from the Embach River. The tails were macroscopically alike and represented a normal tail with respect to fins, integumentum, and muscles.

The accessory tails were always postanal and smaller than the normal tail. The point of origin varied; the extra tails occurred on dorsal, ventral, or lateral surfaces (Fig. 1). Some of the extra tails were misshaped and curled, but others were normal in shape and pigment pattern.

Other abnormalities in larval sea lampreys were malformed or twisted tails and bodies. Of the 8437 examined, eight had crooked or kinked bodies, four had deformed or curled tails, and four lacked the entire postanal section of the body. McLain (1952) reported the absence of the postanal section of the body in one of 215 recently metamorphosed sea lampreys. No abnormalities other than the extra caudal fins were noted among the other species of lampreys.

The cause of the structural abnormalities is unknown. The presence of extra caudal

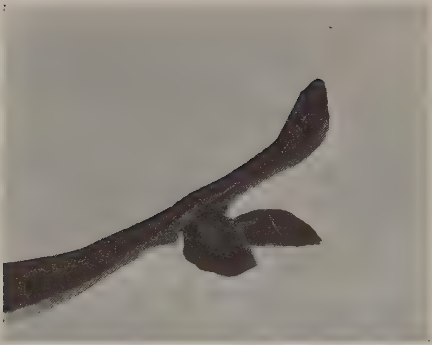

Fig. 2. A recently metamorphosed *Petromyzon marinus* (123 mm total length) with three tails.

fins could be genetically controlled, or be due to partial amputation or injury followed by abnormal regeneration. Niazi (1963, 1964) has shown that all tissues in the caudal area of ammocetes are capable of regeneration. Barfurth (1899) hypothesized that additional tails were developed through regeneration after injury.

Few if any lampreys with structural abnormalities live to sexual maturity. None of the abnormalities found in lamprey larvae were observed among approximately 258,000 adult sea lampreys taken at electric barriers operated in Lake Superior in 1953–60 in an attempt to control the sea lamprey (McLain, Smith, and Moore, 1965).

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Eggs and Early Larval Stages of the Offshore Hake, *Merluccius albidus*

Of the ten species of *Merluccius* occurring on the coasts of the American continents (Ginsberg, 1954), the eggs and larvae of only three species have been described: *M. bilinearis* (Mitchill) by Kuntz and Radcliffe (1917), *M. gayi* (Guichenot) by Fischer (1959), and *M. productus* (Ayres) by Ahlstrom and Counts (1955). *Merluccius albidus* (Mitchill) was not distinguished from *M. bilinearis* by recent authors until 1954 (Ginsburg, 1954). As the distribution and spawning time of these two sympatric species overlap, it is possible that some of the eggs and larvae previously identified as *M. bilinearis* were, in fact, *M. albidus*. The purpose of this note is to describe the eggs and early larval stages (to 84 hours after hatching) of *M. albidus* and compare these with those of *M. bilinearis*.

Ripe and running offshore hake (one female, three males) were trawled by the *Albatross IV* south of Martha's Vineyard, 40°03′ N–70°23′ W, on 26 April 1963. Previous data (Bigelow and Schroeder, 1955) have shown that ripe females were present in this area during June 1953 and July 1954.

Table 1.—*Characters which aid in distinguishing the eggs and newly hatched larvae of* M. albidus *and* M. bilinearis

	Merluccius albidus	*Merluccius bilinearis*[1]
Egg		
Size	1.10 mm (0.99 to 1.18 mm)	0.88 to 0.95 mm
Oil globule	0.32 mm (0.29 to 0.36 mm)	0.19 to 0.23 mm
Pigmentation:		
Yolk	Anterior—near head and posterior near oil globule	None
Embryo	Scattered on head and body after tail is partially separated from yolk	Scattered on head and body soon after blastophore closure
Newly hatched larvae		
Size	3.54 (3.05 to 3.75 mm)	2.8 mm
Pigmentation:		
Yolk	Anterior—near head and posterior near oil globule	None
Head	A group in jaw region and back of head	Sparsely scattered over the head and anterior trunk region
Body	A concentration dorsal to yolk sac and over vent	

[1] Characteristics from Kuntz and Radcliffe, 1917.

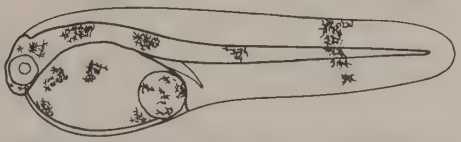

Figure 1.—*Merluccius albidus* at hatching, total length 3.5 mm.

Artificially fertilized eggs were incubated in hatching jars kept in a water bath at a temperature of 48–51 F. Water in the jars was changed daily, at which time a sample of eggs (and, after hatching began, prolarvae) was preserved in 2.5% neutral formalin. All measurements and descriptions of eggs and larvae were made within two weeks of preservation.

The fertilized *M. albidus* egg is pelagic, spherical, transparent, and has a narrow perivitelline space. The average diameter (100 eggs) was 1.10 mm (range 0.99 to 1.18 mm). There was no measurable difference in size between live and preserved eggs. The single oil globule averaged 0.32 mm (range 0.29 to 0.36 mm). These egg and oil globule diameters are slightly larger than those of *M. bilinearis*: egg 0.88 to 0.95 mm, oil globule 0.19 to 0.23 mm (Kuntz and Radcliffe, 1917). The egg and developing embryo of the offshore hake are colorless until after the tail has partially separated from the yolk mass. Pigmentation is found soon after blastopore closure in *M. bilinearis* (Kuntz and Radcliffe, 1917), and immediately after in *M. productus* (Ahlstrom and Counts, 1955). At this stage of development small stellate melanophores are visible on the body, yolk mass (none in *M. bilinearis*), and oil globule. These melanophores coalesce into patches as the embryo develops. The distribution of the pigment patches remains the same from late stage embryo to newly hatched larva (Figure 1). Table 1 has been included to facilitate the comparison of eggs and newly hatched larvae of *M. albidus* and *M. bilinearis*.

All larvae hatched between 6 and 8 days after fertilization. *Merluccius albidus* hatches in a relatively undeveloped condition; it begins its postembryonic existence before the

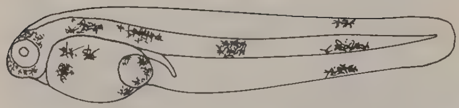

FIGURE 2.—*Merluccius albidus* 84 hours old, total length 3.9 mm.

mouth forms or the eyes become pigmented. At hatching, the length of prolarvae averaged 3.54 mm and ranged from 3.05 to 3.75 mm (*M. bilinearis* hatches at approximately 2.8 mm, Kuntz and Radcliffe, 1917). The vent opens laterally near the middle of the ventral finfold, a short distance behind the yolk sac. The prolarvae have a group of melanophores in the jaw region and on the posterior part of the head. The body has four distinct concentrations of pigment: dorsal to the yolk sac; over the vent; at the midpoint of the trunk; and two-thirds of the distance to the tail. The last is a band of melanophores extending onto the dorsal and ventral finfold. Large melanophores are also present on the anterior part of the yolk mass, and scattered on the oil globule. The distribution of pigment on the head, yolk mass, and body distinguishes these prolarvae from those of *M. bilinearis* (Kuntz and Radcliffe, 1917). Although the size and number of melanophores vary slightly, their distribution was about the same for all specimens during the first 84 hours of growth. The gradual absorption of the yolk, decrease in size of the oil globule, and elongation of the body are the only readily discernible changes during this period of development (Figure 2).

It is possible that this prolarval pigmentation pattern changes in later stages as it does in *M. bilinearis* and *M. productus*, therefore this pigment pattern may not be diagnostic for postlarvae.

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Oceanographic Program of the Bureau of Commercial Fisheries in the Pacific Ocean

by

J.C. Marr

Reprinted from Proceedings of the 1967 Pacific Command Oceanographic Conference,
Camp H.H. Smith, Hawaii, 1967

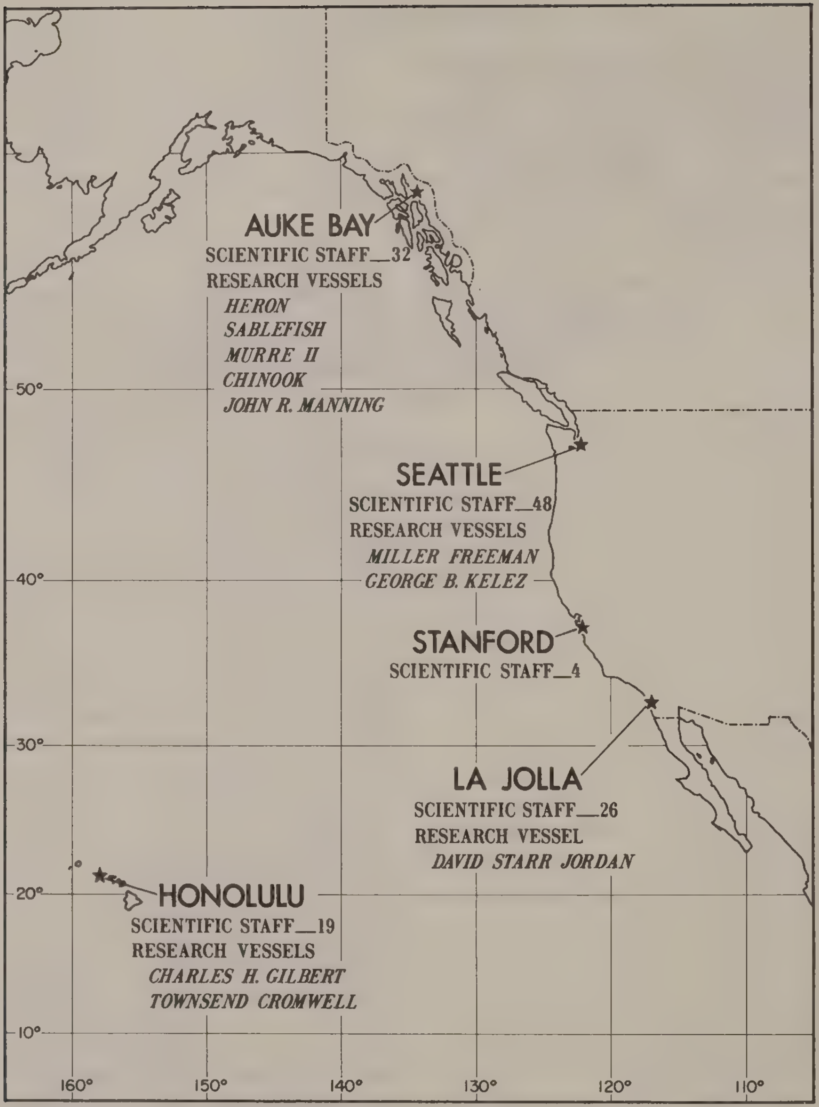
AUKE BAY
SCIENTIFIC STAFF__32
RESEARCH VESSELS
HERON
SABLEFISH
MURRE II
CHINOOK
JOHN R. MANNING
SEATTLE
SCIENTIFIC STAFF__48
RESEARCH VESSELS
MILLER FREEMAN
GEORGE B. KELEZ
STANFORD
SCIENTIFIC STAFF__4
LA JOLLA
SCIENTIFIC STAFF__26
RESEARCH VESSEL
DAVID STARR JORDAN
HONOLULU
SCIENTIFIC STAFF__19
RESEARCH VESSELS
CHARLES H. GILBERT
TOWNSEND CROMWELL
50°
40°
30°
20°
10°
160°
150°
140°
130°
120°
110°

PLATE A.2-1 Location of Bureau of Commercial Fisheries laboratories concerned with Pacific Oceanography

OCEANOGRAPHIC PROGRAM OF THE BUREAU OF COMMERCIAL FISHERIES IN THE PACIFIC OCEAN

by

J. C. Marr,
Bureau of Commercial Fisheries

INTRODUCTION

Like the Navy, the Bureau of Commercial Fisheries has a mission-oriented research program. Broadly speaking, the mission of the Bureau is to identify and to bring into production fishery resources and to maintain this production at levels of maximum sustained yields. These fishery resources may be those belonging to the United States--that is, those confined to the territorial sea and the contiguous fishing zone--or they may be common-use resources, those of the high seas.

The accomplishment of this mission involves an almost unbelievable array of activities ranging from physical oceanography and fishery biology through vessel and gear design, food processing, marketing, and economics, to international relations. Today, of course, I am concerned primarily with the oceanographic interests of the Bureau. Since fishes and ships both tend to occur in the upper layers of the ocean, it is obvious that the Navy and the Bureau share many oceanographic interests. It doesn't take much imagination, for example, to think of features in common between the problems of looking for submarines and the problems of looking for fish.

Thus, it is not surprising that there is already a great deal of cooperation and exchange of information between the Navy and the Bureau. Conferences such as this one may be most valuable in bringing to our mutual attention additional opportunities for fruitful inter-agency cooperation.

PACIFIC LABORATORIES

Among the Bureau establishments located near the Pacific, five are concerned with oceanographic problems. These include the biological laboratories at Auke Bay, Alaska; Seattle, Washington; Stanford and La Jolla, California and Honolulu, Hawaii. I shall briefly describe the particular oceanographic interests of each. Since I am most familiar with the Honolulu Laboratory, and since it covers a somewhat larger area, both physically and perhaps scientifically, I shall deal at greatest length with its activities.

[Plate A.2-1] In Plate 1 are shown the locations of these laboratories, the number of professional scientists on their staffs, and the number of research vessels employed.

Auke Bay Laboratory

Although the Auke Bay Laboratory is concerned with a variety of fishery resources in the Gulf of Alaska and the Bering Sea, oceanographic studies are limited by the lack of facilities and in part because relevant studies in the Gulf of Alaska are being carried out by the Seattle Laboratory. As a consequence, the present oceanographic work of the Auke Bay Laboratory is in what may be called coastal oceanography. Additional observations are received from Coast Guard light stations and Coast and Geodetic Survey tide stations. Information on the transport through the Bering Strait is received from the Navy Electronics Laboratory. Data on the transport through Unimak Pass would be very useful, as would a Bering Sea array of buoys which would provide information on wind speed and direction and on air and sea temperatures.

Seattle Laboratory

Primarily because of interest in salmon--interest involving international problems as well as the problems of salmon ecology--the Seattle Laboratory has participated extensively in the study of the currents of the North Pacific north of 40° N., largely through the method of standard hydrographic sections.

Considerable effort has gone into the use of monitoring buoys. Present models employ temperature sensors accurate to ±0.02° C. and pressure sensors accurate to 1 percent of depth. Provision has been made to accommodate salinity, oxygen, and irradiance sensors when sensors with satisfactory accuracy and long-term stability are available. The buoys sample the sensors on command or according to a pre-set schedule. The data are stored on magnetic tape in a binary format for transmission upon interrogation. Active buoy life is 1 year. These buoys are designed as free-floating instruments and there is the obvious problem of determining location. It is planned for this purpose to use satellites through IRLS (interrogation, recording, location system) or TRANSIT.

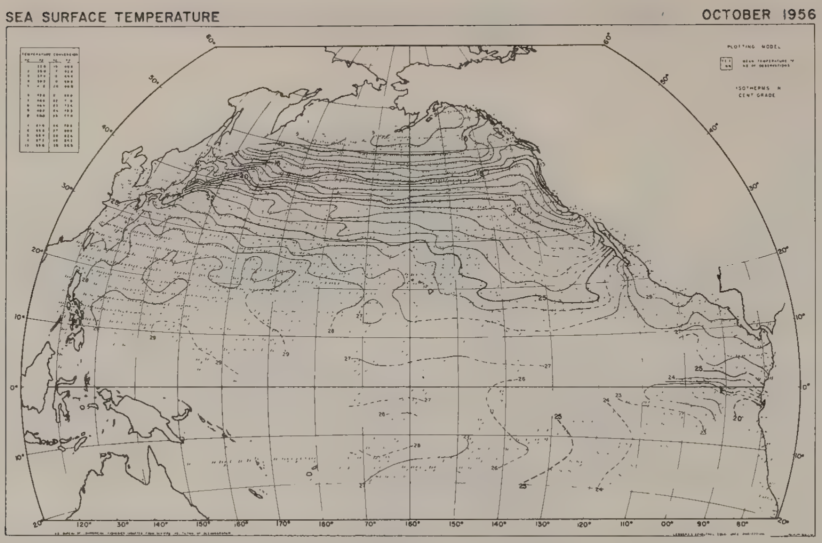
SEA SURFACE TEMPERATURE
OCTOBER 1956
20°
10°
0°
10°
20°
30°
40°
50°
60°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°

PLATE A.2-2 North Pacific sea surface temperature, October 1956.

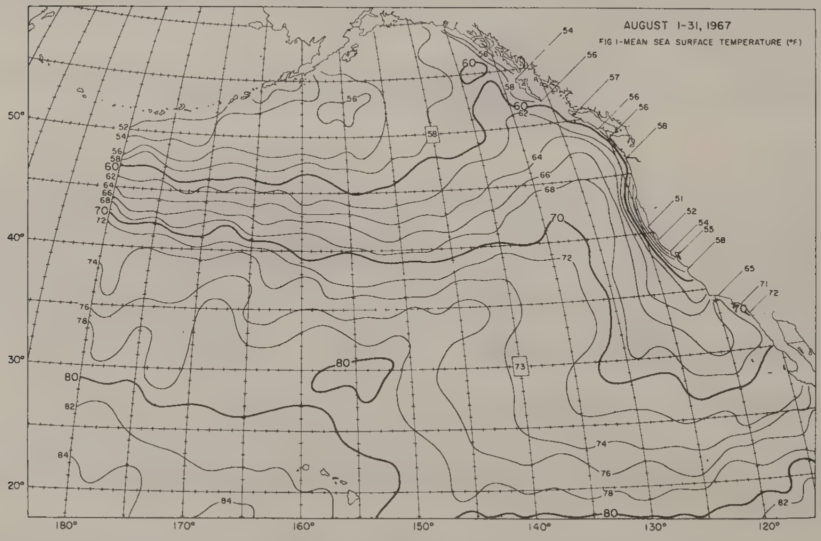
AUGUST 1-31, 1967
FIG 1-MEAN SEA SURFACE TEMPERATURE (°F)
50°
40°
30°
20°
180°
170°
160°
150°
140°
130°
120°
60
70
80

PLATE A.2-3 Mean sea surface temperature, August 1967.

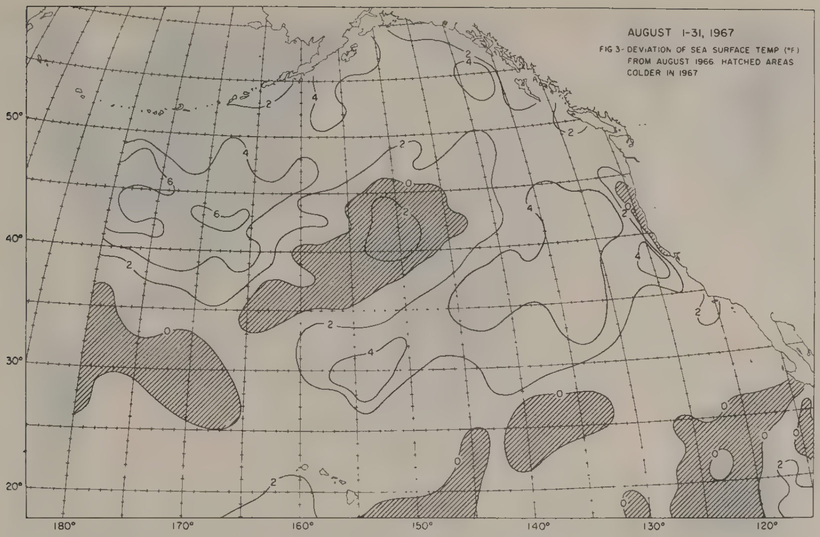
AUGUST 1-31, 1967
FIG 3- DEVIATION OF SEA SURFACE TEMP (°F) FROM AUGUST 1966. HATCHED AREAS COLDER IN 1967
50°
40°
30°
20°
180°
170°
160°
150°
140°
130°
120°

PLATE A.2-3a Deviation of sea surface temperature August 1967 from 1966

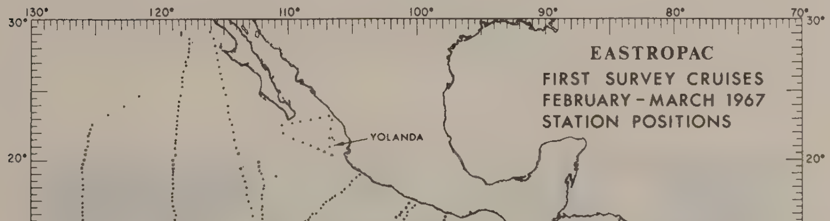
EASTROPAC
FIRST SURVEY CRUISES
FEBRUARY - MARCH 1967
STATION POSITIONS
YOLANDA
ALAMINOS
DAVIS
UNANUE
YELCHO
ARGO
JORDAN
ROCKAWAY
130°
120°
110°
100°
90°
80°
70°
30°
20°
10°
0°
10°
20°

PLATE A.2-4 Cruise tracks, EASTROPAC first survey cruises.

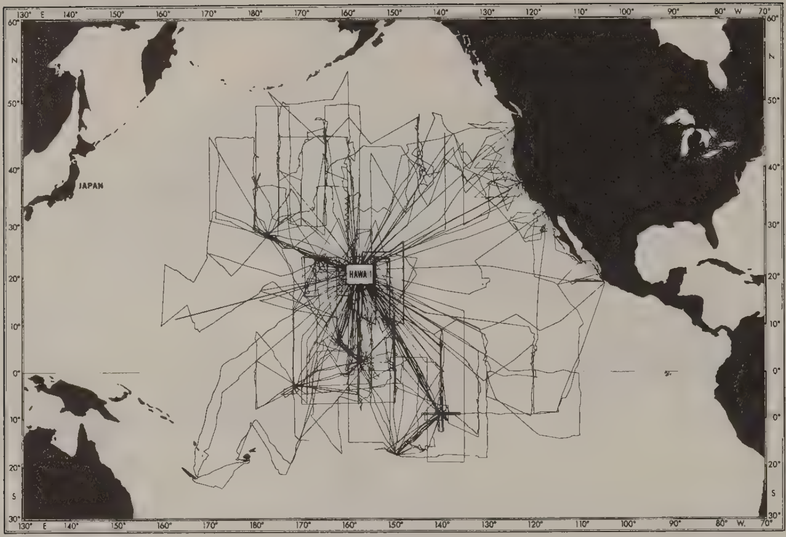
JAPAN
HAWAII

PLATE A.2-5 Tracks of cruises carried out by BCF Honolulu Laboratory.

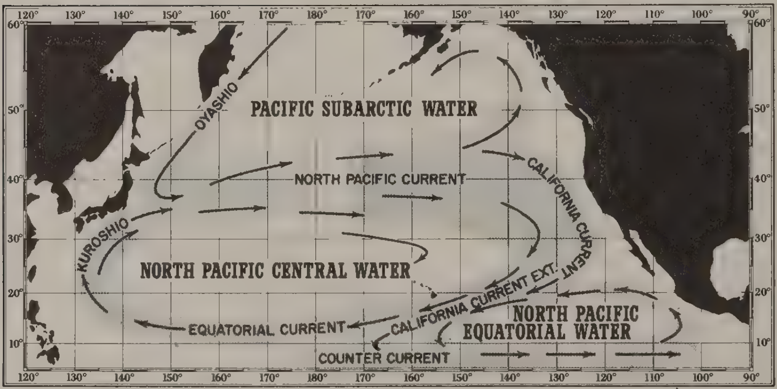
OYASHIO
PACIFIC SUBARCTIC WATER
NORTH PACIFIC CURRENT
CALIFORNIA CURRENT
KUROSHIO
NORTH PACIFIC CENTRAL WATER
CALIFORNIA CURRENT EXT.
CALIFORNIA CURRENT
NORTH PACIFIC EQUATORIAL WATER
EQUATORIAL CURRENT
COUNTER CURRENT

PLATE A.2-6 Circulation of the North Pacific

Stanford Laboratory

The main interest of the Stanford Laboratory is in the causes of relatively long-term changes in the distribution and abundance of fishery resources. These changes are unrelated to the direct effects of fishing and are believed to be associated with changes in the environment. Much effort has therefore been devoted to compiling in a useful form historical data series on surface temperatures in the North Pacific. These particular data have been derived primarily from the observations of merchant ships. As an example of these summaries, Plate 2 shows the surface temperature of the North Pacific for October 1956. [Plate A.2-2] These data have also been expressed as the change from the same month of the preceding year. One atlas for the years 1956 and 1957 has already been published and the series will eventually cover a 14-year period starting with 1950. Much of this and other work of the Stanford Laboratory has been carried out in close cooperation with the Fleet Numerical Weather Facility in Monterey.

Considerable interest exists in increasing the quantity and quality of what might be called monitoring data, through island stations, ships of opportunity, and instrumented buoys. Some work has already been done on the use of XBT's (expendable bathythermograph) by merchant ships.

La Jolla Laboratory

Tuna fisherman find useful charts of sea surface temperatures, provided they are available on a reasonably "real-time" basis. Such charts, originally developed by the Honolulu Laboratory, are issued as a service function by the La Jolla Laboratory. [Plate A.2-3] An example is shown in Plate 3. These charts are produced monthly, except that during the albacore and bluefin tuna season off the west coast they are issued twice monthly. The charts are available shortly after the end of the reporting period. Here again, cooperation with the Fleet Numerical Weather Facility, as well as other institutions, is close.

A major cooperative oceanographic study in which the La Jolla Laboratory is deeply involved is EASTROPAC. This is a seasonal survey of the area from 20° S. to 30° N. and from 130° W. eastward to the coast of the Americas. [Plate A.2-4] The cruise tracks are shown in Plate 4. In addition to the La Jolla Laboratory, EASTROPAC has involved the Scripps Institution of Oceanography, Coast Guard, Navy Oceanographic Office, Texas A & M, ESSA, University of Miami, and others. Following the seasonal survey cruises, planned cruises will study specific oceanographic problems and carry out exploratory fishing.

Honolulu Laboratory

The Honolulu Laboratory is concerned with the fishery resources--primarily tunas--of the tropical and subtropical Pacific and the relation of these resources to their environment. [Plate A.2-5] In Plate 5 are shown the tracks of cruises carried out by the Laboratory. As an example of oceanographic studies carried out by the Laboratory, I may mention that of the Pacific equatorial circulation, including the discovery of the Cromwell Undercurrent. As an example of studies relating the resources to their environment, I may mention the association of the local skipjack tuna fishery with the seasonal oscillations of the California Current Extension. [Plate A.2-6] I call your attention in Plate 6, to the boundary between the North Pacific Central Water and the California Current Extension. This boundary moves through the Hawaiian Island chain, south in the winter and north in the summer. If the movement of the boundary is such that the northward movement commences fairly early in the year and the northward extent coincides with the islands, the skipjack fishery in the summer months is good. If these conditions are not met, the fishery is poor. Through observations from our monitoring station at Koko Head on Oahu, we are able to predict this condition several months in advance of the fishing season and have done so for the past several years.

I would like to mention three oceanographic studies of particular interest to this conference. The first is a study of circulation in the Hawaiian Islands or, more accurately, the local effects of the Hawaiian Islands on the circulation in the central Pacific. The second is a summary of the existing station data of the entire Pacific Ocean. And the third is a cooperative study, known as Porpoise, of the rates of change of important oceanographic processes in the major energy-input area of the Pacific

Island Effects

The Hawaiian Islands constitute a large barrier imposed on the circulation pattern of the North Pacific. As might be expected, such a barrier produces interesting effects of the kind shown in Plate 7. [Plate A.2-7] The upper panel shows the theoretical eddy formation downstream from the island of Hawaii; the lower panel shows the structures observed on a 1953 cruise of the R/V *Hugh M. Smith*. Based on observations made during this and more recent cruises, it is known that

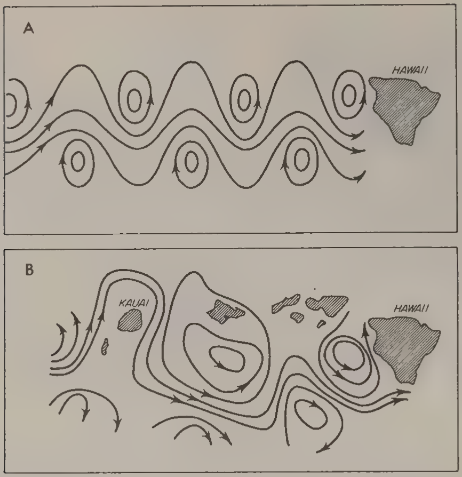
A
HAWAII
B
KAUAI
HAWAII

PLATE A.2-7 Upper panel: Theoretical eddy formation downstream from Hawaii. Lower panel: Dynamic topography observed in March 1953.

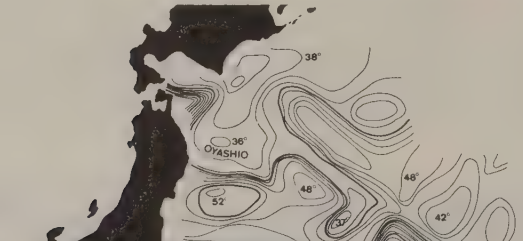
38°
36°
OYASHIO
48°
52°
48°
37°
42°
36°
TOKYO
KUROSHIO
66°
OYASHIO
WARM
COLD
WARM
COLD
WARM
COLD
KUROSHIO
TOKYO

PLATE A.2-8 Upper panel: Temperatures at 200 m. in the Kuroshio-Oyashio region. Lower panel: Theoretical vortex street model developed to account for the currents and other major features of the Kuroshio-Oyashio front.

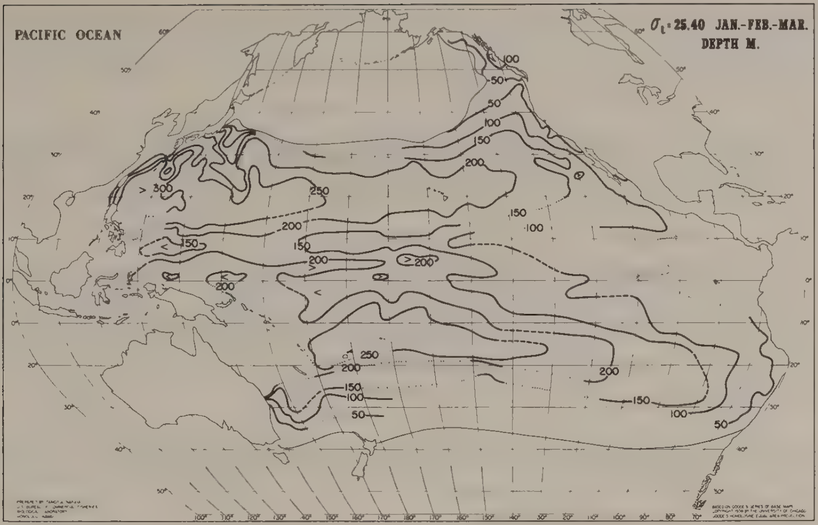
PACIFIC OCEAN
σ_t = 25.40 JAN.-FEB.-MAR.
DEPTH M.
100
50
50
100
150
200
> 300
250
200
150
100
150
150
200
> 200
< 200
250
200
150
100
50
200
150
100
50

PLATE A.2-9 Depth of the 25.40 sigma-t surface for the quarter January-March

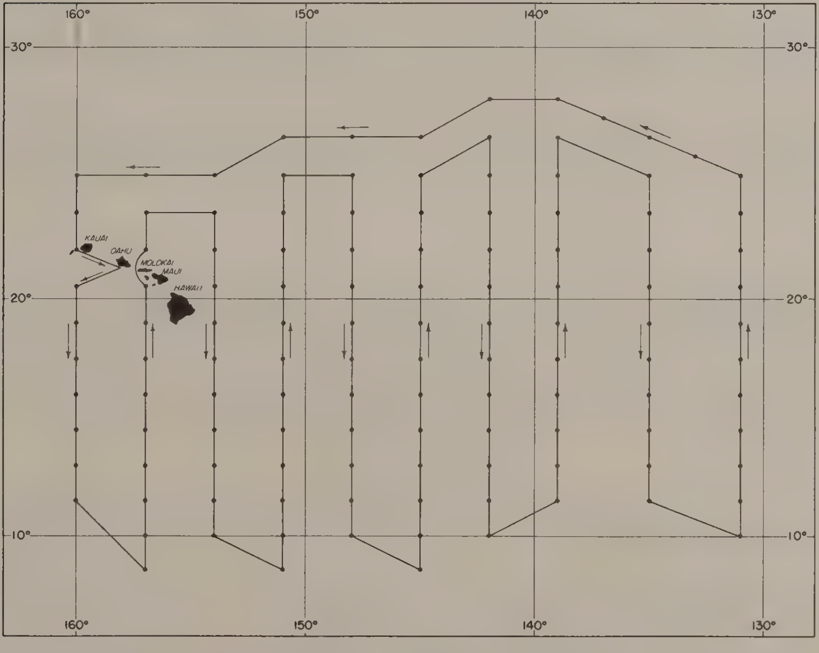
160°
150°
140°
130°
30°
20°
10°
KAUAI
OAHU
MOLOKAI
MAUI
HAWAII

PLATE A.2-10 Porpoise cruise tracks.

these eddies form alternately in counter-rotating sequence in the lee of Hawaii, grow until they attain the approximate dimension of the island (that is, about 80 miles in diameter), and then either remain stationary for some time or move off downstream at the rate of about 6 miles per day. A particular eddy may persist downstream for 12 weeks, at which time it would be about 480 miles from its origin.

It is believed that these eddies are, in fact, a von Karman wake. Dr. Barkley, who has been carrying out these studies, has also examined the Kuroshio-Oyashio interface, as is shown in Plate 8. [Plate A.2-8] Here there appears to be a double wake, or what he has termed a von Karman street.

Pacific Atlas

All of the available oceanographic station data in the Pacific through 1964 have been summarized in a series of charts. As an example, one of these is shown in Plate 9. [Plate A.2-9] As you will note, the properties are shown in relation to sigma-t surfaces. The atlas has a total of 156 charts and about two-thirds of them are in the form of sigma-t surfaces. As allowed by the density of observations, the data were averaged by 1° squares and by quarters of the year. I should mention that the data were obtained from NODC and copies of our tapes have been made available to the Fleet Numerical Weather Facility.

These charts will be published in the form of an atlas by the University of Hawaii Press. The atlas is scheduled to be available in March 1968. Again, this study has been carried out by Dr. Barkley.

Porpoise

Porpoise is an intensive study of the area shown in Plate 10. [Plate A.2-10] Its genesis is in the work of Mr. Seckel, which has been published as *Atlas of the Oceanographic Climate of the Hawaiian Islands Region* and in a series of 16 monthly cruises carried out by the R/V *Townsend Cromwell* in part of the Porpoise area during 1964-65. The atlas proposed a climatic model of the oceanographic processes in the central Pacific and the repetitive cruises demonstrated that the time and space patterns of the proposed observations will permit testing of the model on a quantitative basis. Porpoise is not a survey. It is the logical next step beyond surveys; an attempt to understand processes, rather than to provide a description of "average" conditions.

Porpoise is planned to start in October 1968 and will require four ships for 14 months; three for oceanographic and meteorological studies and one for fishery studies. Two ships will be supplied by the Bureau. Other institutions involved include the Navy Oceanographic Office, University of Hawaii, and the Smithsonian Institution. It is hoped that ESSA and the Coast Guard will also participate.

SUMMARY

The Bureau of Commercial Fisheries, through five biological laboratories located near the Pacific, has a wide variety of interests in oceanography. I have indicated some of these, dealing, I hope with permissible provincialism, at greatest length with those of the Honolulu Laboratory. It is obvious that these interests correspond in large part with those of the Navy, with respect to geographic areas, vertical extent, and particular properties. It is also obvious that extensive cooperation between the Bureau and the Navy already exists. I am sure that mutually beneficial areas for additional cooperation will become apparent during this meeting.

DISCUSSION PERIOD

Q. On these programs, what would be the maximum depth of the observations?
A. I think the maximum is 1500 meters going to the bottom at the corners of the pattern.

Q. You mentioned that when the northern boundry of the equatorial current doesn't progress as far north as the average, then the fish are not as abundant. Where are the fish during those years?
A. That's a good question. We don't know where the fish are when they are not here. We have tagged thousands of skipjack tuna in and around Hawaii and we only have a few recoveries two or three years later.

[Reprint, from *Symposium on Scombroid Fishes, Part III*]

RESEARCH PROGRAMME OF THE U.S. BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY, HONOLULU, HAWAII

RESEARCH PROGRAMME OF THE U.S. BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY, HONOLULU, HAWAII

John C. Marr[1]

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The research programme of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[2] is designed to further knowledge of the high seas fishery resources, especially the tunas, in the central tropical and subtropical Pacific Ocean, of the ocean in which these fishes live, and, especially, of the interaction between fish and ocean.

Largely as a matter of convenience, the work in progress is grouped in six units ; Oceanography, Fishery Potentials, Skipjack Ecology, Albacore Ecology, Behaviour, and Subpopulations.

Oceanography : All of the oceanographic station data of the Pacific (about 40 per cent of which are now on hand) are being examined to determine (1) average conditions, (2) annual and seasonal variations from the average, and (3) areas in which additional observations are needed. The computing facilities (IBM 650 computer and satellite equipment) of the University of Hawaii are being used in these studies, which would otherwise be prohibitive in terms of man-hour requirements. In addition to their intrinsic interest, the results of these studies are expected to be of value in studies of fish distribution, abundance, spawning areas, subpopulation location, etc.

A recent study of all of the oceanographic data available from a 3 million square mile area around the Hawaiian Islands, plus heat budget considerations, led to the description of the oceanographic climate of the area and the hypothesis that the major observed annual changes are due to advection. A 2-year period of intensive observations in the area is planned in order to test the hypothesis (as well as some of the assumptions in the heat budget calculations) and to measure the rates at which the oceanographic processes occur. The results will also be useful in understanding the seasonal movements of skipjack in the Hawaiian Islands area (see below).

Interesting results were obtained from drift bottle releases in the Hawaiian Islands area during three cruises in 1961. All releases were made under conditions of prevailing Northeast Trade Winds. Recoveries from releases made in the late winter, when the Trade Winds were weak, showed movement from the leeward side of the island chain to the windward side (i.e., movement of the surface waters against the wind), with no recoveries from bottles released to the east and north of the islands. Recoveries from releases in the spring, when the Trade Wind circulation was strong, were similar, with recovery localities extending farther to the northwest. Recoveries from releases in the summer tended to be just the reverse, with recoveries from bottles released to windward, but few from releases to leeward. The possibility of aircraft drops, rather than releases from surface craft, will be investigated, since these will permit more frequent and synoptic coverage of the area at reduced cost.

Temperature and salinity data from monitoring stations have been found to be of increasing value as the length of the time series and the number of stations increase. Land stations now extend from Samoa to Midway and from Wake to the Hawaiian Islands. Data are also obtained from North Pacific Weather Ships.

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[2] Formerly known as the Pacific Oceanic Fishery Investigations,

Studies of both invertebrate and vertebrate indicator species over a large area of the Pacific are in progress.

Fishery Potentials : Determination of tuna yield and, especially, estimates of maximum yield may be based on catch data and information on growth, age, and mortality rates. Efforts are being made to compile catch data for those tuna fisheries of the Pacific for which the data are not now readily available.

Accumulation of size data, by sexes, for certain species of tunas has revealed sexual dimorphism in growth. In bigeye tuna, for example, males grow faster than females, so that there is an excess of males at larger sizes. In Hawaii, at least, the sex ratio (in the catch) changes during the course of the year. Differences such as these must be taken into account in maximum yield estimates.

Skipjack Ecology : Owing to the seasonal nature of the occurrence of skipjack, the Hawaiian Islands constitute a natural laboratory for the study of the relationship of skipjack to their environment. Although skipjack occur in the vicinity of Hawaii throughout the year, the larger fish (18-22 lbs.) are most abundant during the summer months, when about 90 per cent of the catch is made. Although tagging experiments have shown that skipjack move freely through the Hawaiian Islands area, their origin is not yet known. It has been observed, however, that their movements are related to oceanographic conditions, with an interesting time lag. In late winter or early spring, the advection of surface water past the island of Oahu changes from a southerly direction to a northerly direction. This change can be simply detected by temperature observations and is signified by the time the surface waters stop cooling and start warming. When this change occurs early in the year, say in early February, the catch of skipjack in the following summer is better than average. When the change occurs in late March, the catch the following summer is less than average.

The nature of this relationship is not yet known. It has obtained over a 10-year period and is used as the basis of predictions to the industry. Predictions not based on understanding may, of course, prove to be disappointing. Major effort on this problem will be devoted to examining all existing data, to see if these suggest a hypothesis which may be tested at sea, and to defining the geographic limits of the subpopulation upon which the Hawaiian fishery is based (see below).

The annual landings of skipjack in the Hawaiian fishery, which is a live-bait fishery, are more frequently limited by live-bait supplies than by the abundance of skipjack. In an effort to alleviate this limitation, experimental fishing trials have been made with monofilament nylon gill nets, using a power block to haul the nets. Although the time available for these trials was inadequate, skipjack can be caught with these nets. At present, it appears that the use of these nets will most likely be complementary to the live-bait fishery, rather than a replacement for it.

Studies of the distribution and abundance of skipjack larvae in Hawaiian waters show a peak of abundance in the summer and a minimum in the winter.

Although the larvae of skipjack and yellowfin have been known for some years, the larvae of other important tuna species have just been identified, including albacore, bigeye, Australian northern bluefin, and Pacific bluefin. It was possible to recognize several kinds of larvae and to assign specific identifications on the basis of the distribution of adults. Owing to differences in the distribution of adults, these identifications appear reasonably firm. Further confirmation will be sought through fertilization attempts at sea.

Albacore Ecology : It has been known for some time, on the basis of tagging experiments that albacore migrate across the North Pacific. The same evidence, however, indicates that this is not a simple, annual trans-Pacific round trip. Consideration of the tagging data and the size distribution of fish in the American coastal fishery (summer), the Japanese west-central longline fishery (winter), and the Japanese coastal fishery (spring) has led to a migration model consistent with the hypothesis of a single North Pacific albacore subpopulation. Briefly stated, it is: Albacore first enter the fishery, probably at age 2, in the American coastal fishery. Fish from the American coastal fishery migrate westward in the fall. Some return to the American fishery the following summer. Others continue westward through the Japanese longline fishery and enter the Japanese coastal fishery. This pattern tends to be age specific, with more of the younger albacore in the eastern Pacific and more of the older albacore in the western Pacific. The mature albacore move south into the spawning grounds, which probably lie in a broad area to the west of Hawaii.

Additional efforts will be made to define the location of albacore spawning grounds in the North Pacific and also in the South Pacific. No albacore tagged in the North Pacific have been recovered in the South Pacific. There is additional evidence (see below) for regarding the South Pacific albacore as distinct from those of the North Pacific. By analogy with the North Pacific, there may be only a single subpopulation of albacore in the South Pacific.

Behaviour : Observation of tuna at sea, through underwater observation ports, has suggested lines of inquiry hitherto impossible. For example, skipjack exhibit a pattern of vertical bars when feeding, in contrast to their usual pattern of horizontal stripes. This suggests a form of communication ; i.e., the behaviour of other skipjack may be influenced upon observing this barred pattern. Similarly, when making dashes for prey, skipjack erect their dorsal fin, displaying the white anterior edge. This fin is also erected when the fish is turning or decelerating.

Experiments with water sprays and different live-bait species showed that catch rates were higher with the water sprays on than when they were off, regardless of the bait species used. However, the feeding rate of skipjack was higher with the sprays on only when a non-diving bait species was used. When diving bait species were used, water sprays had no effect on feeding rate.

In live-bait fishing it is common, in some area, to encounter what have been considered to be mixed schools of skipjack and yellowfin. Recent observations on a few such encounters revealed that, in reality, these were independent schools of yellowfin and skipjack which momentarily converged on the same prey and then proceeded on their separate ways.

Improvement in handling techniques has made it possible to maintain skipjack in tanks for as long as 5-1/2 months, thus permitting behaviour studies under controlled conditions. Skipjack prove to be easily conditioned to respond to stimuli, and experiments are in progress to determine their visual acuity and colour discrimination. Anatomical studies of sensory systems will be made. The olfactory capsule is presently being examined.

Observations have shown that shrimp exoskeletons began to appear in the faces in as short a period as 1-1/2 hours after skipjack were fed shrimp. It is a common experience of fishermen that they are most likely to catch fish in the early morning or late afternoon. Experiments in which skipjack were fed to satiation at hourly intervals show a peak in feeding rate in early morning and in the afternoon. The morning peak was much greater than the afternoon peak.

Subpopulations : The problem of identifying discrete population units, or subpopulations, has long been recognized as a pressing one in fishery biology. Unfortunately, the techniques available have yielded less than the desired results for most marine fishes. Morphometric and meristic characteristics are frequently modified by environmental conditions. Tagging experiments may be difficult to design so that they will yield the desired information. There is needed a characteristic known to be under genetic control and capable of defining subpopulations. Blood group systems constitute such a characteristic.

Considerable time has been spent in developing reagents capable of recognizing blood group systems in tunas. Most effort has been expended on skipjack and albacore, but the studies are now being expanded to include yellowfin, bigeye, billfishes, and some of the pelagic sharks, Results thus far show the existence of distinct subpopulations of skipjack in the Hawaiian Islands and in the Marquesas Islands. Similarly, albacore samples from the North Pacific and South Pacific are distinct. As results accumulate, it will be possible to consider the population dynamics of discrete subpopulations, the ecological situations associated with subpopulation divergence, etc.

Studies on the genetics of blood group systems in tilapia are in progress.

In conclusion, I wish to mention the existence of special facilities of the Laboratory, including (1) its location in the Trade Wind zone of the Pacific, (2) the local availability of several species of tunas, (3) underwater observation ports in the research vessel *Charles H. Gilbert*, and (4) extensive collections of zooplankton and bathypelagic fishes. Visiting investigators are welcome.

Made in United States of America
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pp. 706–707

NEW PLASTIC DRIFT CARD

Glass drift bottles have been used successfully to study the currents in surface waters of lakes and oceans for many years. The glass bottles, however, have the serious disadvantages of being heavy, bulky, and breakable.

Many attempts have been made to overcome these disadvantages. Olson (1951) enclosed printed cards in plastic envelopes that were weighted to float upright. Barkley, Ito, and Brown (1964), who compared returns from drift bottles and drift envelopes used in the central North Pacific, indicated that the two devices gave similar results. They proposed a modification of Olson's design that was intended to reduce sinking from leaks caused by faulty construction and damage by birds. In experiments off South Africa, Duncan (1965) found that drift envelopes were punctured and abraded on rocky beaches. He developed a small laminated plastic drift card to overcome this problem, but this card lies flat on the surface of the water and is therefore greatly affected by strong winds.

A satisfactory drift device must be minimally affected by wind and maximally affected by water currents. It should be lightweight, compact, durable, resistant to damage by animals, highly visible, and inexpensive.

The Bureau of Commercial Fisheries has developed a drift card (for studies of the coastal currents of southeastern Alaska and their relation to salmon migrations) that seems to meet these requirements. This card (Fig. 1) is printed on a rectangular sheet of international orange colored plastic (22 × 28 cm). Each sheet is numbered and folded in half lengthwise. A float of expanded polystyrene (0.8 × 2.5 × 7.5 cm) is attached along the inside of the fold, near one end, with two staples (stainless steel staples are recommended for long-term ocean studies). A 3.5-g lead weight is attached with a staple inside the fold at each of the two corners diagonal from the float. The two edges opposite the fold are kept apart by the float and the resilience of the plastic along the fold.

The folded drift card measures 11 × 28 cm and weighs about 22 g. It floats with about 3 cm of the folded edge above the water and the top corners of the opposite edges just under the water (*see* Fig. 1). The exposed triangular portion of the card is cocked by the wind so that the folded edge of the card rotates into the wind. At the same time the edges of the card opposite the fold are forced farther apart as the card moves downwind through the water. This position produces maximum drag in the water.

The outer surface of the card bears printed instructions to the finder. One part is an addressed, postpaid postcard (which must be cut out by the finder) with appropriate instructions and space for recording data.

The J. L. Darling Corporation of Tacoma, Washington, adapted the design for mass production and filled the first order. The initial price of $0.17 per card should decrease as production increases.

Initial returns from the first extensive use of the new drift cards are encouraging. Between 17 and 27 May, 17,000 cards were distributed in southeastern Alaska and

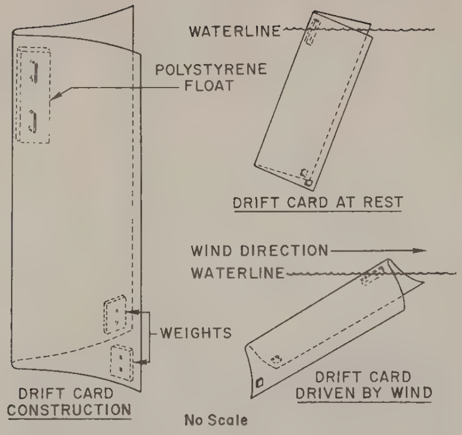

Fig. 1. The plastic drift card of the Bureau of Commercial Fisheries. The diagrams show construction details, position of drift card at rest in the water, and the card opened toward the direction of wind drift.

within 3 weeks more than 300 had been returned. Many of the cards had been found drifting by fishermen. Often the whole drift card was returned, and these were examined for defects and damage. The only serious problem is the electrolytic decay of the zinc-coated staples used to attach the weights to the cards. This resulted in loss of the weights after 4 or 5 weeks. The staples that fasten the floats to the cards showed little corrosion. Splitting has been noted along the fold on some cards—a quality control problem reported by the manufacturer. The effectiveness of the drift cards is not seriously affected by this splitting because it is limited to the portion below the float. Recoveries from wave-washed rock beaches have occasionally been cracked across the card, but there is no measure of the full damage that can be done. An additional 20,000 drift cards, scheduled for distribution in southeastern Alaska this summer, are being manufactured with modifications to reduce corrosion of staples and splitting and cracking of the card.

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Made in United States of America
Reprinted from Copeia, 1967, No. 4, December 8
pp. 837–838

THE FIRST RECORD OF BLACK SKIPJACK, *EUTHYNNUS LINEATUS*, FROM THE HAWAIIAN ISLANDS.—There are three allopatric species in the genus *Euthynnus*—*E. alletteratus* (Rafinesque) in the Atlantic, *E. affinis* (Cantor) in the Indo-western Pacific, and *E. lineatus* Kishinouye in the eastern Pacific. Of the two Pacific forms, there is only one record of *E. affinis* in the eastern Pacific (Fitch, 1953). The black skipjack, *E. lineatus*, heretofore has been recorded only from the coastal waters of Mexico, Central America, northern South America, and the Galápagos Islands (Kishinouye, 1923; Godsil, 1954). The first known occurrence of this species outside this area (in the Hawaiian Islands) is recorded in this note.

The specimen black skipjack, 500 mm FL, a female with early maturing gonads, was caught from a mixed school of skipjack tuna (*Katsuwonus pelamis*) and small bigeye tuna (*Thunnus obesus*) by live-bait fishing, on cruise 93 of the U. S. Bureau of Commercial Fisheries research vessel, Charles H. Gilbert, on 19 July 1966, approximately 56 km W of the island of Hawaii. The fish appeared to be in good condition; although its weight was not recorded, the ratios of body width and depth to body length were well within the ranges given by Godsil and Byers (1944).

Measurements (in mm) taken according to the methods described by Godsil and Byers and counts are as follows: Fork length—500; head length—144; 1st dorsal insertion—155; 2nd dorsal insertion—291; anal insertion—326; ventral insertion—157; greatest body depth—120; greatest body width—84; dorsal–ventral distance—114; dorsal–anal distance—207; ventral insertion to vent—164; length 1st dorsal base—143; length 2nd dorsal base—32; length of anal base—30; pectoral length—85; height of 1st dorsal—66; height of 2nd dorsal—36; height of anal—40; diam-

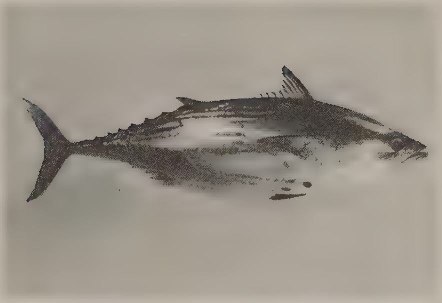

Fig. 1. Black skipjack (*Euthynnus lineatus*) 500 mm FL, caught off the Hawaiian Islands.

eter of iris—21; maxillary length—55; snout to posterior margin of eye—59.

Counts: 1st dorsal spines—15; 2nd dorsal rays—12; dorsal finlets—8; anal rays—12; anal finlets—7; gill rakers—8 + 1 + 25 = 34.

External characters agree with Godsil's (1954) description of the species. Five black unbranched stripes run horizontally on the back from the corselet to the caudal fin, and five or six faint unbranched stripes run horizontally on the belly (Fig. 1). The stripes on the belly fade out before they reach a vertical through the anus. Two black thoracic spots are situated at the indentation of the corselet and one spot each at the dorsal end of the gill cleft and at the posteroventral margin of the orbit. The 12th, 13th, and 15th spines in the first dorsal fin were deeply imbedded and were found only after dissection.

The internal characters also agree with Godsil's (1954) description of the species. The only difference is that this specimen has a smaller caecal mass than that shown by Godsil and the apex of the caecal mass projects slightly over half the length of the viscera.

Distinctive of the species are 37 vertebrae (20 precaudal + 17 caudal) and four large vertebral protuberances on the 31st vertebra. These protuberances or lobes are formed by the enlargement of the anterior end of the centrum. Godsil (1954) found considerable variation in the extent of development of these lobes. In our specimen the four lobes are equally developed and the 30th vertebra also carries three smaller lobes—one dorsal and two ventral to the caudal keel.

This capture poses several interesting questions about the species. Is the species distributed over an area wider than previously known? Is this fish a chance migrant from the eastern Pacific Ocean? Does this capture indicate the beginning of a movement of the species out of its known habitat? These questions can be answered only with more captures in the future.

We thank Vernon E. Brock and William A. Gosline for their review of this manuscript.

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PACIFIC SALMON LITERATURE COMPILATION--1900-59
INSTRUCTIONS AND INDEX

By

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ABSTRACT

Expanding research on the Pacific salmon with resultant increase in publications has created literature problems for the fishery scientist. The purpose of the compilation, totaling 645 microfiches, is to make published scientific information on the five North American species of Pacific salmon immediately accessible and usable. The compilation contains 1,406 articles on original research comprising 17,895 pages of text from 119 serials, journals, and reports. The text material was analyzed and items of information were coded according to an outline of subject categories. The pages of text are duplicated as many times as different items of information under these subject categories are contained in the text. With these duplications the material totals some 42,341 pages under 4,000 subject categories. Each item is arranged by author and date of publication. Instructions for finding information on a subject are given in the introductory text.

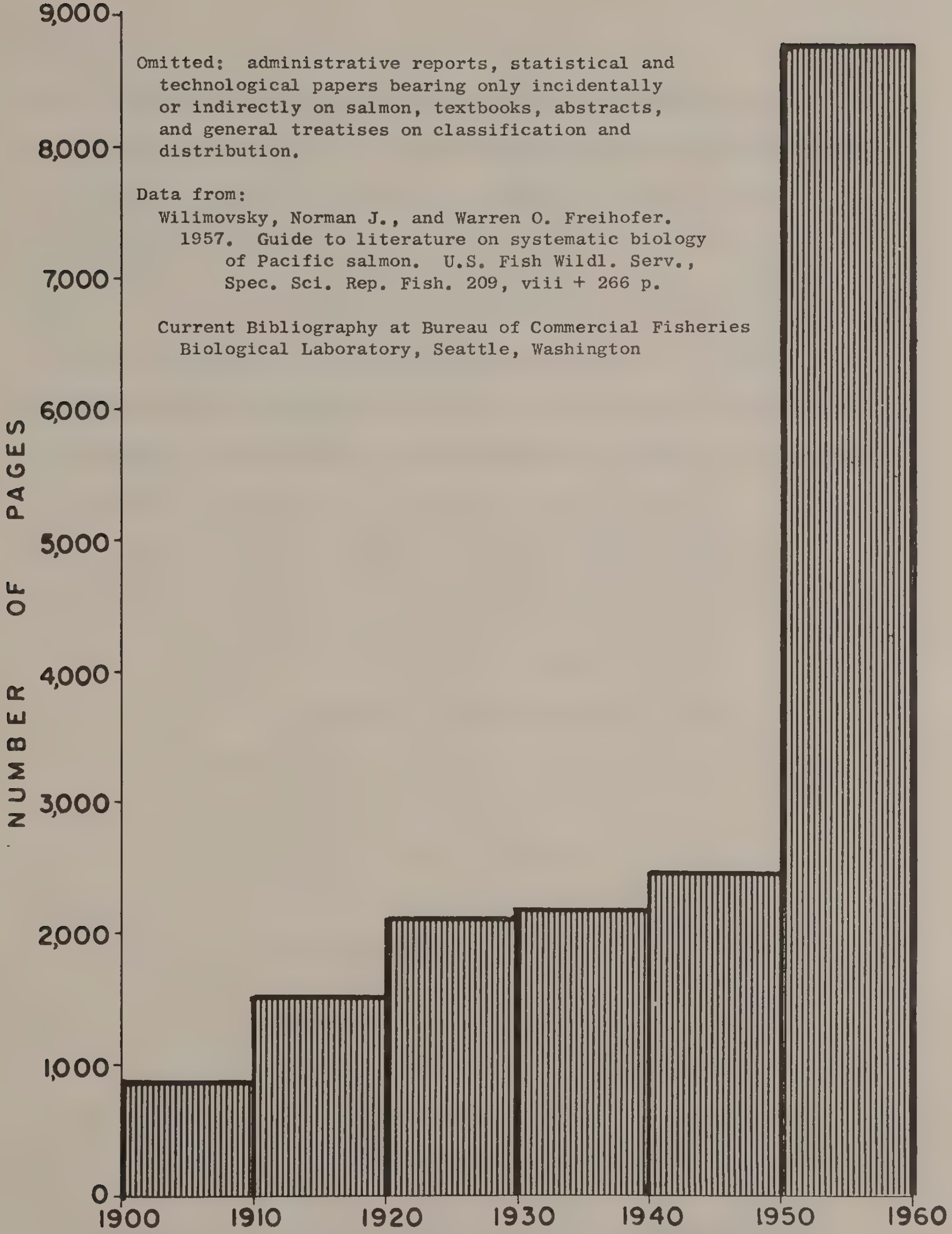
Reprinted from U.S. Department of Commerce, Clearinghouse for Federal Scientific and Technical Information, PB 174 101, April 1967

INTRODUCTION

The number of publications on the Pacific salmon (genus Oncorhynchus) has increased greatly in recent years. The size of this increase is evident in a bar chart (see page 3) showing, by 10-year periods, the number of pages of scientific literature published on Pacific salmon from 1900 through 1959 that have been included in this compilation. Significantly, there were 3½ times as many pages published during the 10 year 1950-59 as in the previous decade. This increasing volume has resulted from expanding research on Pacific salmon by governmental agencies, commissions, and universities because of the urgency of problems of management and conservation.

A library has difficulty in trying to obtain all the original reports, which are so numerous and diverse. With constantly expanding research in fishery biology, the incomplete library of today will be even more incomplete tomorrow. Only large centralized libraries with adequate staffs can even attempt to keep pace with the proliferating literature. Fishery biologists who lack ready access to such libraries may develop a narrow outlook and be less than knowledgeable in fishery science. Providing comprehensive and penetrating material would help the scientist avoid unnecessary repetition of research and enable him to plan his investigations better.

The purpose of this compilation is to make published scientific information on the Pacific salmon immediately accessible and usable.



Omitted: administrative reports, statistical and technological papers bearing only incidentally or indirectly on salmon, textbooks, abstracts, and general treatises on classification and distribution.

Data from:

Wilimovsky, Norman J., and Warren O. Freihofer. 1957. Guide to literature on systematic biology of Pacific salmon. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 209, viii + 266 p.

Current Bibliography at Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington

Total pages of scientific literature on Pacific salmon by 10-year periods.

Scope

This compilation has 1,406 articles comprising 17,895 pages of text. These articles were compiled from 119 serials, journals, and reports. The compilation has three restrictions: (1) It covers publications on the five North American species of Pacific salmon (*Oncorhynchus keta*, *O. tshawytscha*, *O. gorbuscha*, *O. nerka*, and *O. kisutch*) and on hybrids of these species (some articles on *O. masou* were collected, but this material has not been included in this compilation); (2) It covers the 60-year period, 1900-59; and (3) It includes only those publications reporting on original scientific research. The coverage is essentially complete for the journals examined; however, not all of the widely scattered single reports in the literature were obtained.

The 17,895 pages of text are duplicated in this compilation as many times as different subjects, or items of information, are contained in the text. (Most of the pages contained three items of information.) These duplications total 42,341 pages. They are arranged by author and date of publication under 4,000 subject headings or categories.

Background

The compilation was originally assembled as duplicate copies of the text pages and used as hard copy. These pages were duplicated and filed over a 3-year period, 1960-63, as a special project by the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.[1] The Bureau's Columbia Fisheries Program Office, Portland, Oreg., provided funds for the project. The work was done in the library of the Fisheries Research Institute, College of Fisheries, University of Washington, Seattle. Special mention must be made of the helpful suggestions of the late William F. Thompson, Professor Emeritus, College of Fisheries, University of Washington, who was a consultant to the project.

Since this set of microfiches is a photographic reproduction of the files of duplicates, our discussion of procedures followed in preparing this compilation will be concerned with the files.

PROCEDURES

Our approach in making items of information, or subjects, in the literature accessible and usable in detail was to: (1) assemble the pages of original text (as noted above); (2) make a duplicate, or "master" copy, of each; (3) analyze the text, coding each item of information according to a logical outline of subjects, or categories, embodied in a system of code numbers (see outline, or code table, entitled, "A System of Classification of Subject Categories for Pacific Salmon," on page 6); (4) make duplicate copies of the coded master sheets, duplicating each master as many times as separate items in the text fitted the subjects and code numbers; and (5) file the duplicates on each subject in a folder labeled with the code number.

1/ These files of duplicates are located at the BCF Biological Laboratory, Seattle. The files--as a unit--often have been called "Pacific Salmon Compendium," which is a misnomer. The correct title for the files is "Pacific Salmon Literature Compilation--1900-59."

Code Table
No. 6 Revision

Pacific Salmon

A System of Classification of Subject Categories

FIRST DIVISION
(Classification)

A (not used)
B Pacific salmon
(Oncorhynchus)
- 0 General
- 1 O. keta
- 2 O. tshawytscha
- 3 O. masou
- 4 O. gorbuscha
- 5 O. nerka
- 6 O. kisutch
- 7 Hybrids

SECOND DIVISION
(Stage of Life)

0 General and inclusive
1 Eggs
2 Fry
3 Fingerlings
4 Seaward migrants
5 Marine stages
6 Spawning migration
7 Spawning
8 Freshwater adults

THIRD DIVISION (Phase of each stage)	FOURTH DIVISION (Specific subjects)
00 General and inclusive	.0 General and inclusive
05 Abundance, numerical	.0 General and inclusive
	.1 Seasons
	.2 Areas
	.3 Counts, estimates
	.4 Sampling
	.5 Age and size groups
	.6 Sex ratios
	.7 Cycles in abundance
10 Age, rates of growth, development	.0 General and inclusive
	.1 Dates of hatching
	.2 Size attained
	.3 Rates
	.4 Nutrition
	.5 Age and size frequencies
	.6 Developmental stages
15 Behavior	.0 General and inclusive
	.1 Manmade obstructions
	.2 Natural obstructions
	.3 Homing
	.4 Migrations (movements)
	.5 Sexual behavior
	.6 Spawning
	.7 Other habits (feeding, predator avoidance, hiding, etc.)
20 Characteristics	.0 General and inclusive
	.1 Anatomy (structural, meristic, or quantitative)
	.2 Biochemistry (composition)
	.3 Physiology (function)
	.4 Color, body shape, markings
	.5 Sense organs
	.6 Sexual dimorphism
	.7 Classification
25 Distributions	.0 General and inclusive
	.1 Geographic
	.2 Within environment (demersal, pelagic, littoral, etc.)
30 Environmental factors (description of factors)	.0 General and inclusive
	.1 Food
	.2 Obstructions, manmade and natural
	.3 Competition (intra- and interspecific)
	.4 Physical factors
	.5 Pollution
	.6 Predators, parasites, and diseases
	.7 Spawning sites (stream surveys, lake surveys)
33 Fisheries - commercial and sport (production and technology)	.0 General and inclusive
	.1 Areas and equipment
	.2 Catches
	.3 Seasons
	.4 Intensity (escapement, selectivity, etc.)
	.5 Regulation
	.6 Technology
35 Mortalities - survivals (effects of factors)	.0 General and inclusive
	.1 Natural factors
	.2 Diseases
	.3 Fishing
	.4 Parasites
	.5 Pollution (silting, chemical, oxygen demand)
	.6 Predation
	.7 Obstruction, manmade and natural
	.8 Miscellaneous human activities (logging, mining, irrigation)
	.9 Theory of population dynamics and models
40 Propagation, aid to, and artificial	.0 General and inclusive
	.1 Hatcheries and fish farms (diseases, food, techniques, etc.)
	.2 Ponds
	.3 Transplantations
	.4 Habitat improvement
	.5 Selective breeding
45 Racial differentiation	.0 General and inclusive
	.1 Racial characteristics
	.2 Genetics (chromosomes, genes, genotypes, etc.)
	.3 Survival value
	.4 Intermixture (during migration, not in breeding)
	.5 Crossing of genetic lines

FIFTH DIVISION
(Descriptive of material)

a Abstracts
b Bibliography, tabulated
d Data, diagrams, and graphs
m Maps
p Pictures
po Programs and organization
t Technique
s Summary
h History, description

Under B in the FIRST DIVISION scientific names are used. Common names encountered in the literature are as follows:

O. keta: Chum or dog

O. tshawytscha: Chinook, king, spring, quinnat, or tyee

O. masou: masu

O. gorbuscha: Pink or humpback

O. nerka: Red, sockeye, blueback, *kokanee, *little redfish

O. kisutch: Silver or coho

*Landlocked form

Final step: File alphabetically by authors under categories of Fourth Division

The code number for each item of information was printed on the margin of the master sheet and opposite the item--a sentence, a paragraph, or a page. The purpose of the code is to make sure that those who analyze the information in the reports will use one system of reference so that all related material will fall into one particular section of a file. Conversely, the code number is analogous to page numbers in a book index.

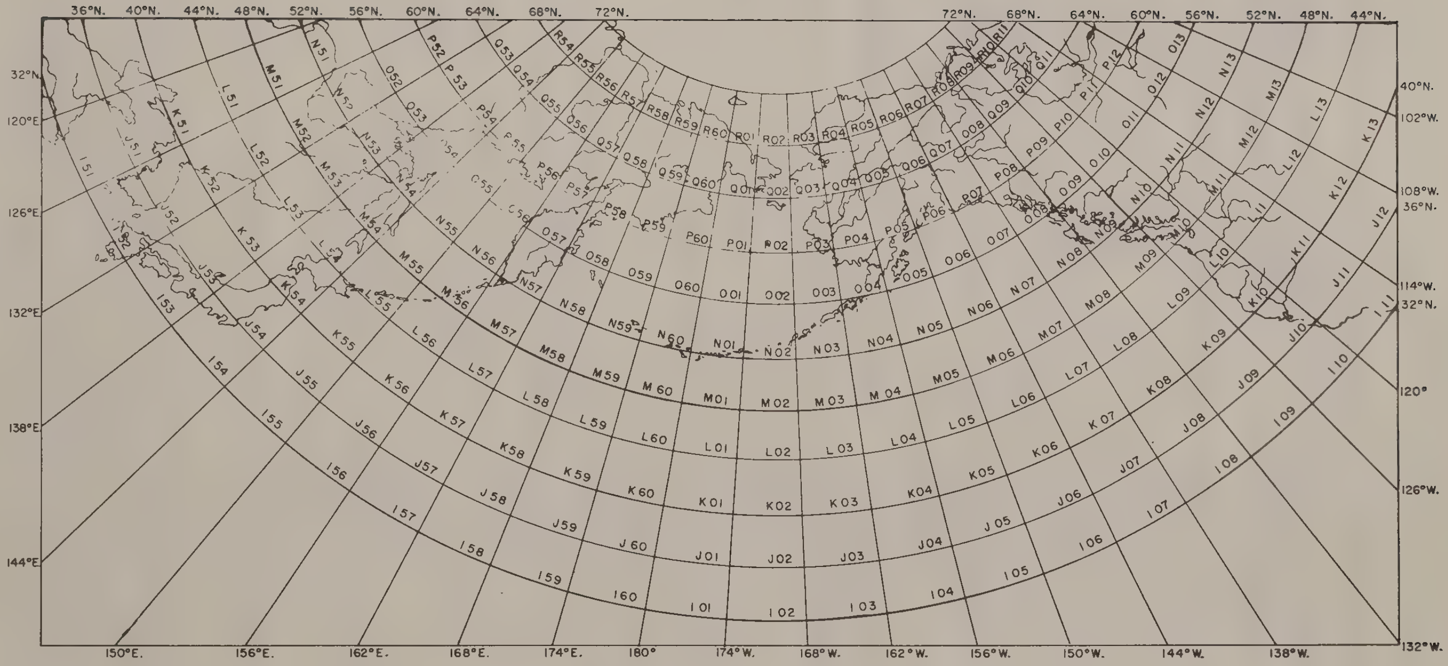
To identify the geographical area where the research reported in the article was done or to locate the area to which the research applied, we used a set of codes based on a system used internationally by geographers. This information is important to the user. (See chart "Geographical Divisions for Locating Research Projects," on page 8). The geographical code designates latitude by capital letters and longitude by two-digit numbers.

A slip with author(s), title, date of publication, source, geographical code, and a list of code numbers (derived in coding all of the subjects found associated in a report) was inserted at the top of each coded master sheet when making the duplicates.

By filing a duplicate copy of a page of original text for each different subject, or item of information, in a folder identified with the code number (i.e., file code), it was possible to bring together pertinent information on a subject from many articles. Each folder thus serves as a literature survey on the subject--the information is accessible and usable in detail in its original text.2/ Most scientists wish to read the original text--not an abstract nor a summary.

A duplicate copy with explanation of format is shown on page 9.

2/ We followed the system of the Human Relations Area File in a modified form in preparing our arrangement of subject headings and code numbers for the Pacific salmon. The Human Relations Area File is sponsored by 16 large universities (including the University of Washington, Seattle, where we examined the File), and is centered at Yale University. This File brings together copies of the original material on every aspect of cultural relations, arranged and coded under headings agreed upon by social scientists. Our outline for the Pacific salmon is much simpler.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52°N.
48°N.
44°N.
32°N.
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126°E.
132°E.
138°E.
144°E.
40°N.
102°W.
108°W.
36°N.
114°W.
32°N.
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150°E.
156°E.
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R09
R10
R11

Geographical divisions for locating research projects, Pacific Salmon Literature Compilation.

DONALDSON, L. R. and F. J. FOSTER 1941

Experimental study of the effect of various water temperatures on the growth, food utilization, and mortality rates of fingerling sockeye salmon. Trans. Amer. Fish. Soc. 70: 339-346.

geographical code ← L10 80.000.0 B5(210.2/215.7/220.2/220.3/ 230.4/235.0/240.1) List of codes for items of information found in article

EXPERIMENTAL STUDY OF THE EFFECT OF VARIOUS WATER TEMPERATURES ON THE GROWTH, FOOD UTILIZATION, AND MORTALITY RATES OF FINGERLING SOCKEYE SALMON

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and

Fred J. Foster
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Abstract

Experiments were conducted with sockeye salmon fingerlings to determine the effect of various water temperatures on the growth, mortality, and food conversion of the fish. Maximum tolerance temperatures were determined, as were the optimum growth zones, as found in Skaha Lake, British Columbia, during the summer and fall months. The experimental data tend to confirm the field observations that young sockeye salmon have a preference for water temperatures similar to those found near the thermocline during the summer and fall months. The temperature of the surface layer of water in the lake was too high for optimum growth, survival, and efficient utilization of food.

Introduction

The sockeye salmon (*Oncorhynchus nerka* Walbaum) is an anadromous fish that spends a part of its life cycle feeding in fresh-water lakes, and a part in the sea. The fresh-water feeding period is usually of one or more years' duration and it is during this fresh-water stage that the species comes directly under the influence of man's activities. The blocking of streams and the consequent prevention of migration to the natural spawning grounds often makes it necessary to transplant the runs of fish to a new environment.

This copy of text was filed under code B5.230.4

Many research workers have assumed that a definite relationship exists between the temperature of the lake water, in which the young sockeye salmon spend their feeding stage, and the well-being and survival of the fish. To date, however, little experimental evidence has become available to serve as a measure of the influence of the water temperature.

B5. 230.4
235.0

The experiments that form the basis of this report were designed to reproduce some of the temperature variations found in lakes that at one time supported runs of sockeye salmon. In addition to the lake temperatures duplicated, additional tanks containing fish were used as controls, and to ascertain the maximum water temperatures the young fish would be able to withstand.

B5.230.4t

Copy of text was also filed under B5.235.0

Pacific Salmon Literature
Coded File
Prepared By
U.S. Fish and Wildlife Service

The duplicates have been filmed for this set of microfiches in the same sequence of code numbers that was established for the individual folders and in the same order that was followed in arranging the individual copies within the folder. (The duplicates were arranged by author and date of publication.)

Whereas the individual folder of duplicates contained material coded to one subject, the individual microfiche often will have reproductions of the contents of several folders. Therefore, the code number sought may lie between two inclusive codes. To aid the user in his search for material in this set, a list of the microfiches with inclusive code numbers has been prepared. The list, which serves as a cross-index from file code to microfiche number, follows some examples on HOW TO FIND YOUR SUBJECT in this set of microfiches.

HOW TO FIND YOUR SUBJECT

To find the original text of the publications in this compilation on a subject having to do with research on Pacific salmon, take the following steps:

1. Frame your inquiry clearly and simply for one subject only, thus: Homing behavior of king salmon (_Oncorhynchus tshawytscha_) _on their spawning migration_.

   Write this down on a piece of paper.

2. Using the outline of subject categories on Pacific salmon that has been printed on page 6 of this microfiche, look for the subject Oncorhynchus tshawytscha in the first column, headed FIRST DIVISION.[3/]

   Find and write down the code number for Oncorhynchus tshawytscha, which is B2. You have coded the species in your inquiry.

3. Add to this the code number 6 from the SECOND DIVISION for stage of life of your species in which you are interested; in this case it is Spawning migration. Your code now reads B2.6 (Spawning migration of king salmon).

4. Add the code number 15 from the THIRD DIVISION for the phase of the stage of life of your species in which you are interested; in this case, it is Behavior. Your code now reads B2.615 (Behavior of king salmon on their spawning migration).

You will note that, thus far, the categories of each division are repeated for each of those of the preceding division: those of the THIRD DIVISION apply to all categories of the SECOND DIVISION; those of the SECOND to all of the FIRST DIVISION. In the FOURTH DIVISION this is no longer so. The specific subjects of this division are grouped under each of the preceding categories of the THIRD DIVISION. Each group is different--that for Behavior is not the same as that dealing with Characteristics or Distribution. The FOURTH DIVISION is therefore nonrepetitive and longest and contains the ultimate subdivision of the files.

[3/] File A was intended for classification and morphology of Salmonidae but not used. The outline is applicable to genera other than Oncorhynchus.

5. Look to the right of code number 15 and, third in order under the FOURTH DIVISION, find a group of specific subject headings. In this group is the subject Homing, with code number 3. Add as above. Your code now reads B2.615.3 (Homing behavior of king salmon on their spawning migration).

6. Look for the microfiche(s) containing the original text coded to B2.615.3. You will find pertinent literature arranged in alphabetical order by authors and by date of publication on two microfiches--Nos. 264 and 265. Your subject matter in this literature is indicated by an arrow pointing to this code number, which is opposite the text sought.

7. Note the complete reference citation of the article reproduced on the top of the page. The first code(s) designates the geographical areas to which the research applies. You also will find a series of code numbers for other subjects dealt with in the report. The entire text can be reconstructed by using this series of code numbers to find the corresponding microfiches containing the coded pages. Or you may use the author-title reference and obtain a copy of the article.

8. You should look for information on your subject under related code numbers, as for example, the code for General, B2.615.0. Or look at material on microfiches coded to B2.615.4, B2.615.5, etc. Other related codes could be B2.715.6 or B2.715.4. As you proceed, such related codes will occur to you. Explore them.

9. Code a second inquiry, using this example: *What data are available on mortalities due to predation on fry of Oncorhynchus tshawytscha?*

Find the code numbers (shown here in parentheses) in:

FIRST DIVISION: Pacific salmon (B) and *O. tshawytscha* (2)

SECOND DIVISION: Fry (2)

THIRD DIVISION: Mortalities (35)

FOURTH DIVISION: Predation (.6)

FIFTH DIVISION: Letter indicating form of presentation of material, data (d)

The code sought is then B2.235.6d. Look for the microfiches bearing this code (Nos. 215, 216, and 217). You should note at this time that the letter code in the *FIFTH DIVISION* is purely descriptive--it indicates the form in which the material is presented--and does not subdivide the material for filing as do the first four divisions.

CROSS INDEX FROM FILE CODE TO MICROFICHE NUMBER

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B0.000.0 - B0.000.0	1	B0.033.5 - B0.035.0	43
B0.000.0 - B0.000.0	2	B0.035.0 - B0.035.1	44
B0.000.0 - B0.000.0	3	B0.035.1 - B0.035.2	45
B0.000.0 - B0.000.0	4	B0.035.2 - B0.035.2	46
B0.000.0 - B0.000.0	5 & 5A	B0.035.2 - B0.035.4	47
B0.000.0 - B0.000.0	6	B0.035.4 - B0.035.4	48
B0.000.0 - B0.005.0	7	B0.035.4 - B0.035.5	49
B0.005.0 - B0.005.7	8	B0.035.5 - B0.035.6	50
B0.005.7 - B0.010.2	9	B0.035.6 - B0.035.6	51
B0.010.2 - B0.015.0	10	B0.035.6 - B0.035.7	52
B0.015.0 - B0.015.0	11	B0.035.7 - B0.035.7	53
B0.015.0 - B0.015.2	12	B0.035.7 - B0.035.8	54
B0.015.2 - B0.015.4	13	B0.035.8 - B0.035.9	55
B0.015.4 - B0.015.4	14	B0.035.9 - B0.040.0	56
B0.015.4 - B0.020.1	15	B0.040.0 - B0.040.1	57
B0.020.1 - B0.020.1	16	B0.040.1 - B0.040.1	58
B0.020.1 - B0.020.2	17	B0.040.1 - B0.040.1	59
B0.020.2 - B0.020.2	18	B0.040.1 - B0.040.4	60
B0.020.2 - B0.020.3	19	B0.040.4 - B0.105.3	61
B0.020.3 - B0.020.3	20	B0.105.3 - B0.130.4	62
B0.020.3 - B0.020.5	21	B0.130.4 - B0.135.1	63
B0.020.5 - B0.025.0	22	B0.135.1 - B0.140.0	64
B0.025.0 - B0.025.2	23	B0.140.0 - B0.140.3	65
B0.025.2 - B0.030.0	24	B0.140.3 - B0.210.2	66
B0.030.0 - B0.030.1	25	B0.210.2 - B0.215.7	67
B0.030.1 - B0.030.2	26	B0.215.7 - B0.230.4	68
B0.030.2 - B0.030.3	27	B0.230.4 - B0.230.5	69
B0.030.3 - B0.030.4	28	B0.230.5 - B0.235.2	70
B0.030.4 - B0.030.4	29	B0.235.2 - B0.240.1	71
B0.030.4 - B0.030.4	30	B0.240.1 - B0.240.1	72
B0.030.4 - B0.030.4	31	B0.240.1 - B0.315.7	73
B0.030.4 - B0.030.5	32	B0.320.1 - B0.335.2	74
B0.030.5 - B0.030.6	33	B0.335.2 - B0.340.1	75
B0.030.6 - B0.030.6	34	B0.340.1 - B0.405.3	76
B0.030.6 - B0.030.7	35	B0.405.3 - B0.415.1	77
B0.030.7 - B0.030.7	36	B0.415.1 - B0.415.1	78
B0.033.0 - B0.033.0	37	B0.415.1 - B0.415.4	79
B0.033.0 - B0.033.1	38	B0.415.4 - B0.420.3	80
B0.033.1 - B0.033.2	39	B0.420.1 - B0.430.4	81
B0.033.2 - B0.033.2	40	B0.430.4 - B0.435.5	82
B0.033.2 - B0.033.4	41	B0.435.5 - B0.435.7	83
B0.033.4 - B0.033.5	42	B0.435.7 - B0.505.2	84

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B0.505.2 - B0.515.4	85	B0.633.5 - B0.635.0	133
B0.515.4 - B0.525.0	86	B0.635.0 - B0.635.5	134
B0.525.0 - B0.530.0	87	B0.635.5 - B0.635.7	135
B0.530.0 - B0.530.4	88	B0.635.7 - B0.635.7	136
B0.530.4 - B0.533.1	89 & 89A	B0.635.7 - B0.640.1	137
B0.533.1 - B0.533.1	90	B0.640.1 - B0.640.3	138
B0.533.1 - B0.533.2	91	B0.640.3 - B0.705.3	139
B0.533.2 - B0.533.2	92	B0.705.3 - B0.720.0	140
B0.533.3 - B0.535.6	93	B0.720.0 - B0.730.4	141
B0.535.6 - B0.605.1	94	B0.730.4 - B0.730.4	142
B0.605.1 - B0.605.1	95	B0.730.4 - B0.740.1	143
B0.605.1 - B0.605.2	96	B0.740.1 - B0.840.1	144
B0.605.2 - B0.605.2	97	B1.000.0 - B1.005.7	145 & 145A
B0.605.2 - B0.605.3	98	B1.005.7 - B1.010.5	146
B0.605.3 - B0.605.3	99	B1.010.5 - B1.025.1	147
B0.605.3 - B0.605.3	100	B1.025.1 - B1.033.1	148
B0.605.3 - B0.615.0	101	B1.033.1 - B1.033.6	149
B0.615.0 - B0.615.1	102	B1.035.0 - B1.105.1	150
B0.615.1 - B0.615.3	103	B1.105.3 - B1.110.6	151
B0.615.3 - B0.615.4	104	B1.110.6 - B1.130.4	152
B0.615.4 - B0.615.4	105	B1.130.4 - B1.135.1	153 & 153A
B0.615.4 - B0.615.4	106	B1.135.1 - B1.210.3	154
B0.615.4 - B0.620.1	107	B1.210.3 - B1.215.4	155
B0.620.1 - B0.620.5	108	B1.215.4 - B1.215.4	156
B0.620.5 - B0.630.2	109	B1.215.4 - B1.220.3	157 & 157A
B0.630.2 - B0.630.2	110	B1.220.3 - B1.230.4	158
B0.630.2 - B0.630.2	111	B1.230.4 - B1.230.6	159
B0.630.2 - B0.630.5	112	B1.230.6 - B1.335.2	160 & 160A
B0.630.5 - B0.630.7	113	B1.335.2 - B1.415.4	161 & 161A
B0.630.7 - B0.630.7	114	B1.415.4 - B1.430.6	162
B0.630.7 - B0.630.7	115	B1.430.6 - B1.515.4	163
B0.630.7 B0.633.0	116	B1.515.4 - B1.520.1	164 & 164A
B0.633.0 - B0.633.1	117	B1.520.1 - B1.533.1	165
B0.633.1 - B0.633.1	118	B1.533.1 - B1.535.1	166
B0.633.1 - B0.633.1	119	B1.535.1 - B1.605.2	167
B0.633.1 - B0.633.1	120	B1.605.2 - B1.605.6	168
B0.633.1 - B0.633.2	121	B1.605.6 - B1.610.5	169 & 169A
B0.633.2 - B0.633.2	122	B1.610.5 - B1.615.4	170 & 170A
B0.633.2 - B0.633.2	123	B1.615.4 - B1.620.2	171
B0.633.2 - B0.633.2	124	B1.620.2 - B1.630.7	172
B0.633.2 - B0.633.2	125	B1.630.7 - B1.633.2	173
B0.633.2 - B0.633.2	126	B1.633.2 - B1.633.2	174
B0.633.2 - B0.633.2	127	B1.633.2 - B1.633.4	175
B0.633.2 - B0.633.2	128	B1.633.4 - B1.715.6	176
B0.633.2 - B0.633.3	129	B1.715.6 - B1.835.2	177
B0.633.3 - B0.633.3	130	B2.000.0 - B2.005.1	178
B0.633.3 - B0.633.4	131	B2.005.1 - B2.010.0	179
B0.633.4 - B0.633.5	132	B2.010.0 - B2.010.3	180

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B2.010.3 - B2.010.5	181	B2.405.1 - B2.405.3	229
B2.010.5 - B2.015.1	182	B2.405.3 - B2.405.5	230
B2.015.1 - B2.015.4	183	B2.405.6 - B2.410.2	231
B2.015.4 - B2.020.1	184	B2.410.2 - B2.415.0	232
B2.020.1 - B2.020.3	185	B2.415.1 - B2.415.4	233
B2.020.3 - B2.025.1	186	B2.415.4 - B2.415.4	234
B2.025.1 - B2.030.4	187	B2.415.7 - B2.430.2	235
B2.030.4 - B2.030.6	188	B2.430.3 - B2.435.5	236
B2.030.6 - B2.033.2	189	B2.435.5 - B2.435.7	237
B2.033.2 - B2.035.0	190	B2.435.7 - B2.435.8	238
B2.035.0 - B2.035.5	191	B2.435.8 - B2.505.3	239
B2.035.5 - B2.040.0	192	B2.505.3 - B2.510.2	240
B2.040.0 - B2.040.3	193	B2.510.2 - B2.510.5	241
B2.040.3 - B2.045.1	194	B2.510.5 - B2.510.5	242
B2.045.1 - B2.105.2	195	B2.510.5 - B2.515.4	243
B2.105.2 - B2.110.3	196	B2.515.4 - B2.515.4	244
B2.110.3 - B2.110.6	197	B2.515.4 - B2.520.1	245
B2.110.6 - B2.120.3	198	B2.520.1 - B2.525.1	246
B2.120.4 - B2.130.4	199	B2.525.1 - B2.530.1	247
B2.130.4 - B2.135.1	200	B2.530.1 - B2.533.0	248
B2.135.1 - B2.135.1	201	B2.533.0 - B2.533.1	249
B2.135.1 - B2.135.8	202	B2.533.1 - B2.533.2	250
B2.135.8 - B2.140.1	203	B2.533.2 - B2.533.2	251
B2.140.1 - B2.140.3	204	B2.533.2 - B2.535.0	252
B2.140.3 - B2.205.3	205	B2.535.0 - B2.605.0	253
B2.205.5 - B2.210.2	206	B2.605.0 - B2.605.1	254
B2.210.2 - B2.210.3	207	B2.605.1 - B2.605.2	255 & 255A
B2.210.3 - B2.215.3	208	B2.605.2 - B2.605.3	256
B2.215.4 - B2.220.1	209	B2.605.3 - B2.605.3	257
B2.220.1 - B2.220.3	210	B2.605.3 - B2.605.3	258
B2.220.3 - B2.230.1	211	B2.605.3 - B2.605.5	259
B2.230.2 - B2.230.4	212	B2.605.5 - B2.610.0	260
B2.230.4 - B2.235.0	213	B2.610.0 - B2.610.2	261
B2.235.0 - B2.235.1	214	B2.610.2 - B2.610.3	262
B2.235.1 - B2.235.2	215	B2.610.3 - B2.610.5	263
B2.235.2 - B2.255.2	216	B2.610.5 - B2.615.3	264
B2.235.2 - B2.240.1	217	B2.615.3 - B2.615.4	265
B2.240.1 - B2.240.1	218	B2.615.4 - B2.615.4	266
B2.240.1 - B2.240.1	219	B2.615.4 - B2.615.4	267
B2.240.1 - B2.240.1	220	B2.615.4 - B2.615.4	268
B2.240.1 - B2.240.3	221	B2.615.4 - B2.620.1	269
B2.240.3 - B2.310.3	222	B2.620.1 B2.620.2	270
B2.310.3 - B2.315.4	223	B2.620.2 - B2.620.3	271
B2.315.4 - B2.320.3	224	B2.620.3 - B2.620.3	272
B2.320.3 - B2.335.0	225	B2.620.3 - B2.630.1	273
B2.335.0 - B2.335.4	226	B2.630.1 - B2.630.2	274
B2.335.4 - B2.340.1	227	B2.630.2 - B2.630.4	275
B2.340.1 - B2.405.1	228	B2.630.4 - B2.630.6	276

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B2.630.6 - B2.630.7	277	B4.405.3 - B4.415.4	325
B2.630.7 - B2.630.7	278	B4.415.4 - B4.435.1	326
B2.630.7 - B2.630.7	279	B4.435.1 - B4.505.0	327
B2.630.7 - B2.630.7	280	B4.505.1 - B4.510.2	328
B2.630.7 - B2.633.0	281	B4.510.2 - B4.525.1	329
B2.633.0 - B2.633.1	282	B4.525.1 - B4.533.1	330
B2.633.1 - B2.633.1	283	B4.533.1 - B4.535.0	331 & 331A
B2.633.1 - B2.633.2	284	B4.535.0 - B4.600.0	332
B2.633.2 - B2.633.2	285	B4.600.0 - B4.605.1	333
B2.633.2 - B2.633.2	286	B4.605.1 - B4.605.3	334
B2.633.2 - B2.633.2	287	B4.605.3 - B4.605.3	335
B2.633.2 - B2.633.4	288	B4.605.3 - B4.605.3	336 & 336A
B2.633.4 - B2.633.5	289	B4.605.3 - B4.605.6	337
B2.633.5 - B2.635.1	290	B4.605.6 - B4.610.2	338
B2.635.1 - B2.635.7	291	B4.610.2 - B4.615.1	339
B2.635.7 - B2.640.0	292	B4.615.1 - B4.615.3	340
B2.640.0 - B2.640.1	293	B4.615.3 - B4.615.4	341
B2.640.1 - B2.640.3	294	B4.615.4 - B4.615.4	342
B2.640.3 - B2.645.1	295	B4.615.4 - B4.615.4	343
B2.645.1 - B2.705.3	296	B4.615.4 - B4.615.4	344
B2.705.3 - B2.705.3	297	B4.615.4 - B4.615.4	345
B2.705.3 - B2.715.6	298	B4.615.4 - B4.625.0	346
B2.715.6 - B2.720.3	299	B4.625.0 - B4.630.4	347
B2.725.0 - B2.730.7	300	B4.630.4 - B4.633.1	348 & 348A
B2.730.7 - B2.730.7	301	B4.633.1 - B4.633.2	349
B2.730.7 - B2.730.7	302	B4.633.2 - B4.633.2	350
B2.730.7 - B2.735.0	303	B4.633.2 - B4.633.2	351
B2.735.0 - B2.740.1	304	B4.633.2 - B4.633.2	352
B2.740.1 - B2.840.0	305	B4.633.2 - B4.633.4	353
B4.000.0 - B4.005.1	306	B4.633.4 - B4.633.5	354
B4.005.1 - B4.010.0	307	B4.633.5 - B4.635.8	355
B4.010.0 - B4.015.4	308	B4.635.9 - B4.705.3	356
B4.015.4 - B4.030.3	309	B4.705.3 - B4.725.1	357
B4.030.3 - B4.033.1	310 & 310A	B4.725.1 - B4.740.1	358
B4.033.1 - B4.035.0	311	B4.740.1 - B4.745.4	359
B4.035.0 - B4.035.1	312	B5.000.0 - B5.000.0	360
B4.035.1 - B4.045.1	313	B5.000.0 - B5.005.0	361
B4.045.1 - B4.110.0	314	B5.005.0 - B5.005.5	362 & 362A
B4.110.0 - B4.135.0	315	B5.005.5 - B5.010.3	363
B4.135.0 - B4.140.1	316	B5.010.3 - B5.010.5	364
B4.140.1 - B4.205.3	317	B5.010.5 - B5.010.5	365
B4.205.3 - B4.210.3	318	B5.010.5 - B5.010.5	366 & 366A
B4.210.4 - B4.215.4	319	B5.010.5 - B5.015.4	367
B4.215.4 - B4.220.1	320	B5.015.4 - B5.020.1	368
B4.220.1 - B4.230.4	321	B5.020.1 - B5.025.2	369 & 369A
B4.230.4 - B4.235.1	322	B5.025.2 - B5.030.1	370
B4.235.1 - B4.305.3	323	B5.030.1 - B5.030.1	371
B4.305.3 - B4.405.3	324	B5.030.1 - B5.030.4	372

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B5.030.4 - B5.030.4	373	B5.415.4 - B5.415.4	421
B5.030.4 - B5.030.7	374	B5.415.4 - B5.420.3	422
B5.030.7 - B5.033.3	375	B5.420.3 - B5.430.1	423
B5.033.3 - B5.035.0	376 & 376A	B5.430.1 - B5.430.4	424
B5.035.0 - B5.035.0	377	B5.430.4 - B5.435.0	425
B5.035.0 - B5.035.4	378 & 378A	B5.435.0 - B5.435.7	426
B5.035.4 - B5.035.7	379	B5.435.7 - B5.435.7	427
B5.035.7 - B5.040.0	380 & 380A	B5.435.7 - B5.505.3	428
B5.040.0 - B5.040.4	381	B5.505.3 - B5.515.4	429
B5.045.0 - B5.045.2	382	B5.515.4 - B5.520.1	430
B5.045.2 - B5.105.3	383	B5.520.1 - B5.530.1	431
B5.105.3 - B5.135.0	384	B5.530.1 - B5.533.2	432
B5.135.0 - B5.135.1	385	B5.533.2 - B5.533.4	433
B5.135.1 - B5.140.0	386	B5.533.4 - B5.605.0	434
B5.140.0 - B5.140.3	387	B5.605.0 - B5.605.1	435
B5.140.3 - B5.205.2	388	B5.605.1 - B5.605.2	436
B5.205.2 - B5.210.0	389	B5.605.2 - B5.605.3	437
B5.210.0 - B5.210.6	390	B5.605.3 - B5.605.3	438
B5.210.6 - B5.215.4	391	B5.605.3 - B5.605.3	439
B5.215.4 - B5.215.7	392	B5.605.3 - B5.605.3	440
B5.215.7 - B5.225.2	393	B5.605.3 - B5.605.3	441
B5.225.2 - B5.230.1	394	B5.605.3 - B5.605.3	442
B5.230.1 - B5.230.4	395	B5.605.3 - B5.605.3	443
B5.230.4 - B5.230.4	396	B5.605.3 - B5.605.5	444
B5.230.4 - B5.233.0	397 & 397A	B5.605.5 - B5.605.5	445
B5.233.5 - B5.235.1	398 & 398A	B5.605.5 - B5.605.5	446
B5.235.1 - B5.235.2	399	B5.605.5 - B5.605.5	447
B5.235.2 - B5.235.6	400 & 400A	B5.605.5 - B5.605.5	448
B5.235.6 - B5.240.1	401 & 401A	B5.605.5 - B5.605.5	449
B5.240.1 - B5.240.1	402	B5.605.5 - B5.605.5	450
B5.240.1 - B5.240.1	403	B5.605.5 - B5.605.5	451
B5.240.1 - B5.305.3	404	B5.605.5 - B5.605.5	452
B5.305.3 - B5.315.4	405	B5.605.5 - B5.605.5	453
B5.315.4 - B5.330.1	406	B5.605.5 - B5.605.5	454
B5.330.1 - B5.330.6	407	B5.605.5 - B5.605.5	455
B5.330.6 - B5.335.2	408	B5.605.6 - B5.605.6	456
B5.335.2 - B5.335.8	409	B5.605.6 - B5.605.6	457
B5.335.8 - B5.405.0	410	B5.605.6 - B5.605.6	458
B5.405.0 - B5.405.3	411 & 411A	B5.605.6 - B5.605.6	459
B5.405.3 - B5.405.3	412	B5.605.6 - B5.605.6	460
B5.405.3 - B5.405.5	413	B5.605.6 - B5.605.6	461
B5.405.5 - B5.410.0	414	B5.605.6 - B5.605.7	462
B5.410.0 - B5.410.2	415	B5.605.7 - B5.605.7	463
B5.410.2 - B5.410.5	416 & 416A	B5.605.7 - B5.610.0	464
B5.410.5 - B5.415.1	417	B5.610.0 - B5.610.2	465
B5.415.1 - B5.415.1	418	B5.610.2 - B5.610.2	466
B5.415.4 - B5.415.4	419	B5.610.2 - B5.610.2	467
B5.415.4 - B5.415.4	420	B5.610.2 - B5.610.2	468

FILE CODE NO.	MICROFICHE NO.	FILE CODE NO.	MICROFICHE NO.
B5.610.2 - B5.610.3	469	B5.635.7 - B5.635.7	517
B5.610.3 - B5.610.5	470	B5.635.7 - B5.835.7	518
B5.610.5 - B5.610.5	471	B5.635.7 - B5.635.7	519 & 519A
B5.610.5 - B5.610.5	472	B5.635.7 - B5.640.0	520 & 520A
B5.610.5 - B5.610.5	473	B5.640.0 - B5.645.0	521
B5.610.5 - B5.610.5	474	B5.645.0 - B5.645.1	522
B5.610.5 - B5.610.5	475	B5.645.1 - B5.645.4	523
B5.610.5 - B5.615.1	476	B5.645.4 - B5.705.1	524
B5.615.1 - B5.615.2	477	B5.705.1 - B5.705.3	525 & 525A
B5.615.2 - B5.615.4	478	B5.705.3 - B5.705.5	526
B5.615.4 - B5.615.4	479	B5.705.5 - B5.710.2	527
B5.615.4 - B5.615.4	480	B5.710.3 - B5.715.6	528
B5.615.4 - B5.615.4	481	B5.715.6 - B5.720.6	529
B5.615.4 - B5.615.4	482	B5.720.6 - B5.730.4	530
B5.615.4 - B5.615.4	483	B5.730.4 - B5.730.7	531
B5.615.4 - B5.615.4	484	B5.730.7 - B5.735.0	532
B5.615.4 - B5.615.4	485	B5.735.0 - B5.735.7	533
B5.615.4 - B5.615.4	486	B5.735.7 - B5.745.4	534
B5.615.6 - B5.620.2	487	B5.745.4 - B5.810.2	535
B5.620.2 - B5.620.2	488	B5.810.2 - B5.820.6	536
B5.620.2 - B5.620.3	489	B5.820.6 - B5.830.4	537
B5.620.3 - B5.620.3	490	B5.830.4 - B5.845.1	538
B5.620.3 - B5.625.2	491	B5.845.1 - B5.845.3	539
B5.630.0 - B5.630.2	492	B6.000.0 - B6.005.3	540 & 540A
B5.630.2 - B5.630.4	493	B6.005.3 - B6.010.3	541
B5.630.4 - B5.630.6	494	B6.010.3 - B6.045.0	542
B5.630.7 - B5.630.7	495	B6.015.4 - B6.015.7	543
B5.630.7 - B5.633.0	496	B6.015.7 - B6.025.0	544
B5.633.0 - B5.633.1	497	B6.025.0 - B6.030.4	545
B5.633.1 - B5.633.2	498	B6.030.4 - B6.033.2	546
B5.633.2 - B5.633.2	499	B6.033.2 - B6.035.0	547 & 547A
B5.633.2 - B5.633.2	500	B6.035.0 - B6.035.6	548
B5.633.2 - B5.633.2	501	B6.035.8 - B6.040.3	549
B5.633.2 - B5.633.2	502	B6.040.3 - B6.110.2	550
B5.633.2 - B5.633.2	503	B6.110.2 - B6.135.5	551
B5.633.2 - B5.633.2	504	B6.135.5 - B6.200.0	552
B5.633.2 - B5.633.2	505	B6.200.0 - B6.210.4	553
B5.633.2 - B5.633.4	506	B6.210.4 - B6.215.4	554
B5.633.4 - B5.633.4	507	B6.215.4 - B6.215.7	555
B5.633.4 - B5.633.4	508	B6.215.7 - B6.220.4	556
B5.633.4 - B5.633.4	509	B6.220.4 - B6.230.4	557
B5.633.4 - B5.633.4	510	B6.230.4 - B6.230.4	558
B5.633.4 - B5.633.5	511	B6.230.5 - B6.235.1	559
B5.633.5 - B5.635.0	512	B6.235.1 - B6.240.0	560
B5.635.0 - B5.635.2	513	B6.240.0 - B6.240.1	561 & 561A
B5.635.2 - B5.635.6	514	B6.240.1 - B6.310.2	562
B5.635.6 - B5.635.7	515	B6.310.2 - B6.315.4	563
B5.635.7 - B5.635.7	516	B6.315.4 - B6.330.6	564

FILE CODE NO.	MICROFICHE NO.
B6.330.6 - B6.335.4	565
B6.335.4 - B6.340.1	566
B6.340.1 - B6.405.0	567
B6.405.0 - B6.405.3	568
B6.405.3 - B6.415.0	569
B6.415.0 - B6.415.1	570
B6.415.2 - B6.415.4	571
B6.415.4 - B6.415.4	572
B6.415.4 - B6.415.7	573
B6.420.0 - B6.430.2	574
B6.430.7 - B6.435.7	575
B6.435.7 - B6.435.7	576
B6.435.7 - B6.435.7	577
B6.435.7 - B6.505.2	578
B6.505.2 - B6.510.2	579
B6.510.2 - B6.515.4	580
B6.515.4 - B6.515.7	581
B6.515.7 - B6.530.1	582
B6.530.1 - B6.533.1	583 & 583A
B6.533.1 - B6.533.2	584
B6.533.2 - B6.533.4	585
B6.533.4 - B6.605.0	586
B6.605.0 - B6.605.2	587
B6.605.2 - B6.605.3	588
B6.605.3 - B6.605.4	589 & 589A
B6.605.4 - B6.610.2	590
B6.610.2 - B6.615.2	591
B6.615.2 - B6.615.4	592
B6.615.4 - B6.615.4	593
B6.615.4 - B6.620.1	594
B6.620.1 - B6.625.0	595
B6.625.0 - B6.630.4	596
B6.630.4 - B6.630.7	597
B6.630.7 - B6.633.0	598
B6.633.0 - B6.633.1	599
B6.633.1 - B6.633.2	600
B6.633.2 - B6.633.2	601
B6.633.2 - B6.633.4	602
B6.633.4 - B6.635.2	603 & 603A
B6.635.2 - B6.700.0	604
B6.705.0 - B6.720.1	605
B6.725.0 - B6.805.6	606
B6.810.0 - B6.845.3	607
B7.000.0 - B7.835.2	608

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THERMAL DOMES IN THE EASTERN TROPICAL ATLANTIC OCEAN[1]

A prominent feature in the subsurface temperature distribution during the southern hemisphere summer (January–April) is a cold water dome off Angola (referred to as the Angola Dome). The shape, location, and thermal distribution of this feature were determined from about 200 bathythermograph and hydrocast temperature observations in the general area of the dome. The data (including Equalant I) were collected by various ships between 1902 and 1963.

Although the distribution of surface temperature does not indicate the presence of the Angola Dome, it is evident on the 20-m surface (Fig. 1) and can be detected as an individual feature to about 150 m.

Indication of the dome may be seen in the *Crawford* bathythermograph section along 8° S lat, prepared by Fuglister (1960). The section crosses the northern sector of the dome near 10° E long. It is also identifiable at three oceanographic stations (322, 323, and 324) of the Ombango Cruise 14, 23 February to 15 April 1961 (Berrit et al. 1963).

The salinities on the 25 g/liter (15–20 m) and 26 g/liter (30 m) sigma-*t* surfaces are lower within the dome than in surrounding waters (35.5‰ as compared with 35.8–36.0‰). This decrease in salinity may be due to a vertical admixture from the surface layer of the low-salinity Congo River water. Donguy, Hardiville, and Le Guen (1965) have shown that the surface isohalines around the Congo Delta are deflected to the southeast. This deflection suggests that Congo water may be entrained by the cyclonic circulation associated with the dome. Dissolved oxygen data from the dome area are scarce, but recorded values are about 2 ml/liter on the 25 and 26 g/liter sigma-*t* surfaces. The low concentration of oxygen at these rather shallow depths may be related to biological activity and, probably, to an upwelling. The Benguela Current, presumably the main source of the water circulating around the dome, has higher concentrations of dissolved oxygen (4–5 ml/liter) to a depth of approximately 100 m (Hart and Currie 1960). The Angola Dome does not exist during the southern hemisphere winter (Fig. 2).

During the southern hemisphere winter there is a thermal dome southwest of Dakar, centered near 10° N lat and 22° W long (Fig. 2). This feature was noticed by Rosignol and Meyrueis (1964) during the June 1962 cruise of the *Gerard Treca* and was named the Guinea Dome. At that time it was about 160 km closer to the shore than in July–September. Changes in position may be expected as the season advances, and anomalies may also be present during individual years. At the 20-m level, a decrease in temperature, salinity, and oxygen is discernible, but the dome is not well developed. It is better developed at 50 m and can be traced to about 200 m. The 25 g/liter sigma-*t* surface is at a depth of about 30 m in the Guinea Dome, compared with a

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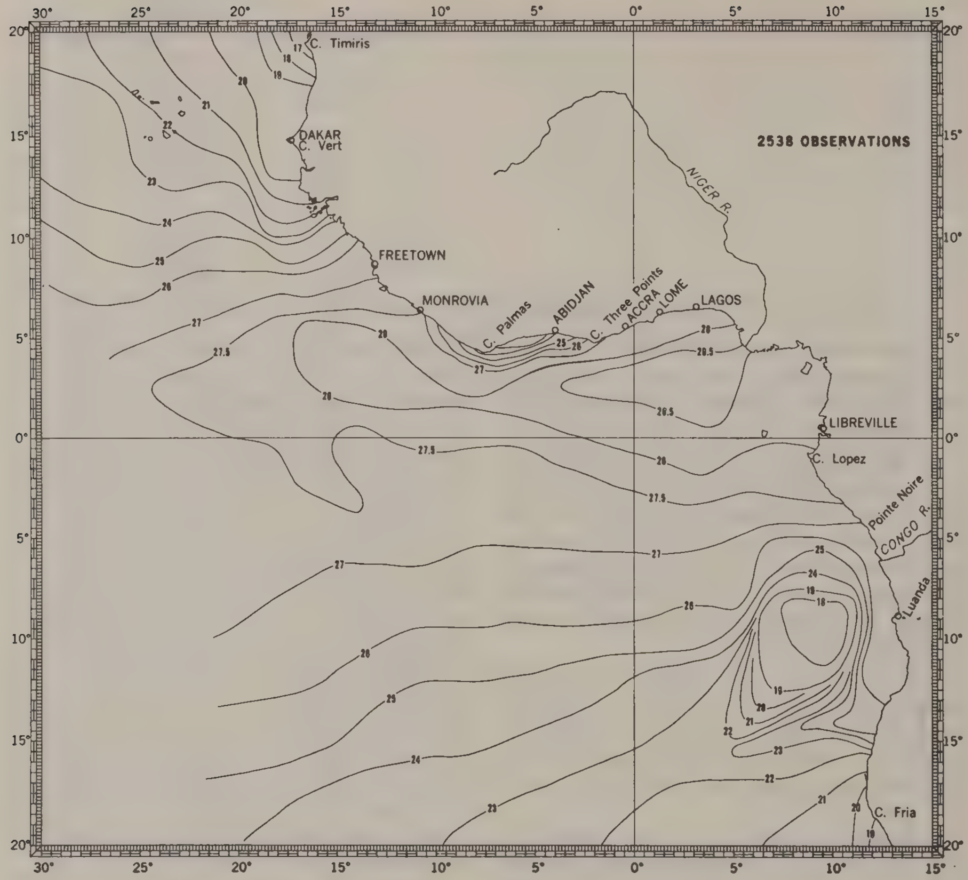
[1] Contribution No. 34, Tropical Atlantic Biological Laboratory, U.S. Bureau of Commercial Fisheries, Miami, Florida 33149.


30°
25°
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20°
C. Timiris
DAKAR
C. Vert
FREETOWN
MONROVIA
C. Palmas
ABIDJAN
C. Three Points
ACCRA
LOME
LAGOS
NIGER R.
2538 OBSERVATIONS
LIBREVILLE
C. Lopez
Pointe Noire
CONGO R.
Luanda
C. Fria

FIG. 1. Temperature (°C) at 20 m during southern hemisphere summer (January–April). Combined BT and station data between 1905 and 1963 (including Equalant I).

depth of about 15 m in the Angola Dome.

A cyclonic circulation around the Guinea Dome appears to be well formed. The geographical distribution of currents around the dome is rather similar to that of the Costa Rica Dome in the Pacific Ocean (Wyrtki 1964). The North Equatorial Current is on the northeast side and, apparently, the northeastward flowing branch of the Equatorial Countercurrent is at the southeast side. Crowding of the isotherms at the southwest side of the dome indicates that a branch of the North Equatorial Current encloses the dome from the southwest, and an enclosed circulation is probably also present on the northeast side.

Another thermal, dome-type elevation is evident during the southern hemisphere winter along 1.5° S lat, extending zonally from about 8° W to 3° E long (Fig. 2). This is an area of intense upwelling associated with a wind-induced divergence of the surface waters. During this season in this zone, the easterly component of the southeast trade winds is predominant. The process of the thermocline elevation and upwelling may be considerably different

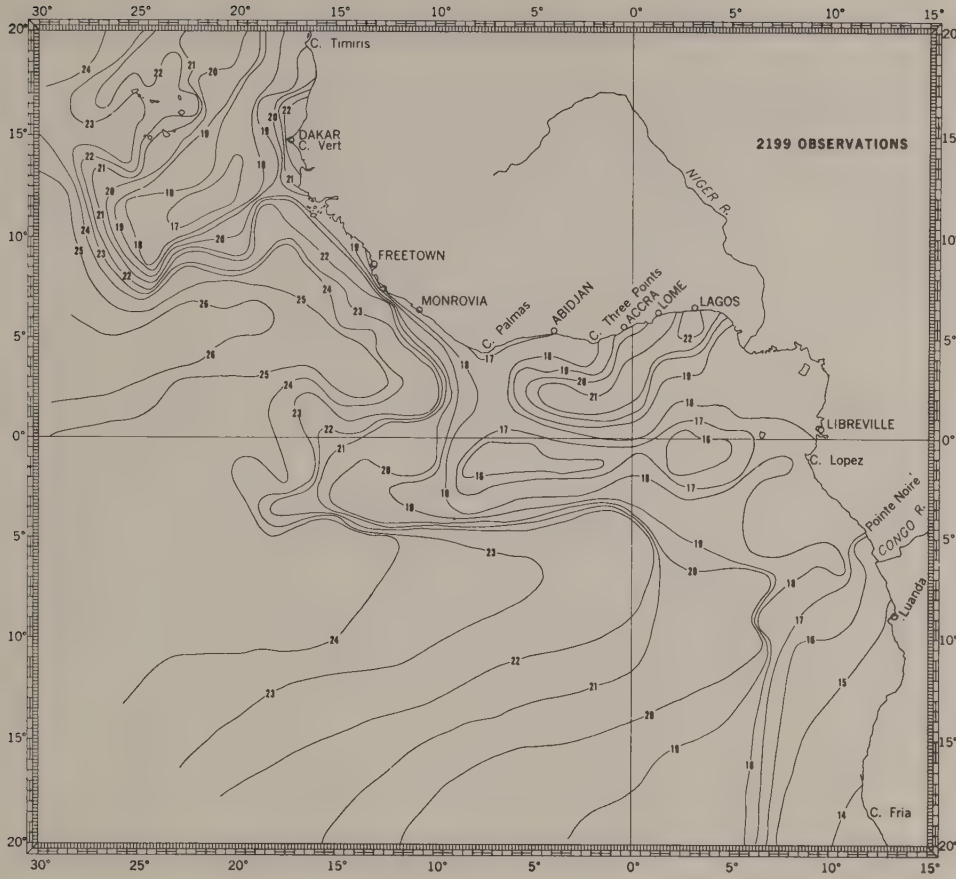
2199 OBSERVATIONS
C. Timiris
DAKAR
C. Vert
FREETOWN
MONROVIA
C. Palmas
ABIDJAN
C. Three Points
ACCRA
LOME
LAGOS
NIGER R.
LIBREVILLE
C. Lopez
Pointe Noire
CONGO R.
Luanda
C. Fria
30°
25°
20°
15°
10°
5°
0°

Fig. 2. Temperature (°C) at 50 m during southern hemisphere winter (July–September). Combined BT and station data between 1905 and 1963 (including Equalant II).

here than in the Guinea and Angola domes.

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A Shrimp Pot for Experimental Fishing

Shrimp of the family Pandalidae are potentially one of Alaska's richest fishery resources. When the U.S. Bureau of Commercial Fisheries began studies of the life histories, ecology, and behavior of these shrimp, shrimp pots were selected as one type of sampling gear. Most of the pots used in commercial shrimp fishing, however, were too heavy and bulky for the research planned. A small, light-weight, circular pot, purchased from a fisherman in Homer, Alaska, was modified, and proved to be effective for experimental use because it captured a large variety of species and a wide range of lengths.

The pots are made with plastic pipe frames, nylon mesh covers, and four tunnel entrances. The materials for each pot cost about $10; a pot can be constructed in 1 hr if the mesh covers are presewn.

A pot with the same basic design but without the tunnel entrances is used for holding live shrimp. These containers are made in a variety of sizes and are excellent for holding shrimp for a year or longer.

Pot Frame. The frame is constructed of $\frac{1}{2}$-inch diam flexible polyethylene plastic pipe (Fig. 1A). The upper and lower hoops are each constructed of four 16-inch pieces of pipe, joined to form a circle with four nylon tees. The two hoops are joined together with four 12-inch pipe uprights. All joints are friction held; no cement or clamps are required. The finished frame is about 22 inches in diameter and 14 inches high. Small holes are drilled in the tees to allow water to fill the hollow frame. When this is done the pot, which weighs 2.2 lb, has slightly negative buoyancy in water. To produce a heavier pot, lead ballast is placed inside the pipe.

Pot Cover. The covering of fine woven nylon mesh has oval openings with a maximum dimension of $\frac{3}{16}$ inch.

Each cover is presewn in two parts — a flat-bottomed, bag-like cover for the bottom and sides of the pot and a flat lid for the top. The cover for the bottom and sides is composed of two pieces of mesh, one a circle the size of the pot bottom (22-inch diam) and the other a rectangular piece as long as the circumference of the frame and somewhat wider than the height of the frame (70 × 17 inches). These are sewn together to form a shallow cylinder with a bottom, and a $\frac{1}{2}$-inch wide nylon elastic band is inserted in a hem around the upper edge. This covering is placed around the frame, and the upper edge is laced to the upper hoop of the frame to hold it firmly in place. The lid is a circle of mesh larger in diameter (approximately 26 inches) than the top of the pot, with a $\frac{1}{2}$-inch wide nylon elastic band inserted in a hem around the edge. The lid fits over the top of the pot and is tied permanently to the upper hoop at three of the tees. This allows the top of the pot to be opened to half of its area without completely removing the lid (Fig. 1B and C.)

Tunnel Entrances. Four tunnel entrances are installed after the pot cover is fastened in place on the frame. Each entrance ring is made of heavy (0.2-

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inch diam) hard-annealed copper wire formed into a circle with a 2½-inch inside diam. The ends of the wire are soldered together to eliminate any gap in the ring. One ring is sewn to the mesh at the center of each of the four sides of the pot (Fig. 1B). After the rings are attached, the mesh within each ring is cut out, and the opposing tunnel rings are pulled together and fastened with twine to form the short tunnels (Fig. 1C).

Other Features of the Pot. A clip is tied to the frame at one of the upper tees (Fig. 1C) to attach the pot to a line for fishing.

Rubber loops cut from tire tubes are fastened to one pair of opposing uprights in the pot frame so that a bait box can be suspended near the center of the pot.

Effectiveness and Durability. The shrimp pots described have been used successfully for research shrimp fishing in Kachemak Bay, Alaska, since 1963. They are generally fished in a long-line arrangement, with several pots attached to a single anchored line. In addition to the usual position on the bottom, these pots can also be fished off bottom because of their light weight. The catch per pot for 24-hr fishing periods is typically over 100 shrimp and has exceeded 600. Most of the shrimp taken are pandalids. The species caught in greatest abundance and the length ranges of their carapaces are:

Species	*Pandalus borealis*	*P. goniurus*	*P. hypsinotus*	*P. platyceros*
Length range (*mm*)	6.0–27.5	5.5–24.0	6.5–40.0	13.0–58.5 .

Shrimp caught in lesser abundance are *Pandalus danae*, *P. stenolepis*, and several species of the family Hippolytidae. A few fish and crabs are also captured.

Since the pots are constructed of noncorroding and nondecaying materials, little maintenance has been necessary. The most frequent repairs have been to torn meshes and to broken or weakened elastic bands in the lid of the pot. With careful handling and a minimal amount of maintenance, these pots can provide an inexpensive and effective method for experimental shrimp fishing.

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(FIG. 1 *opposite*)

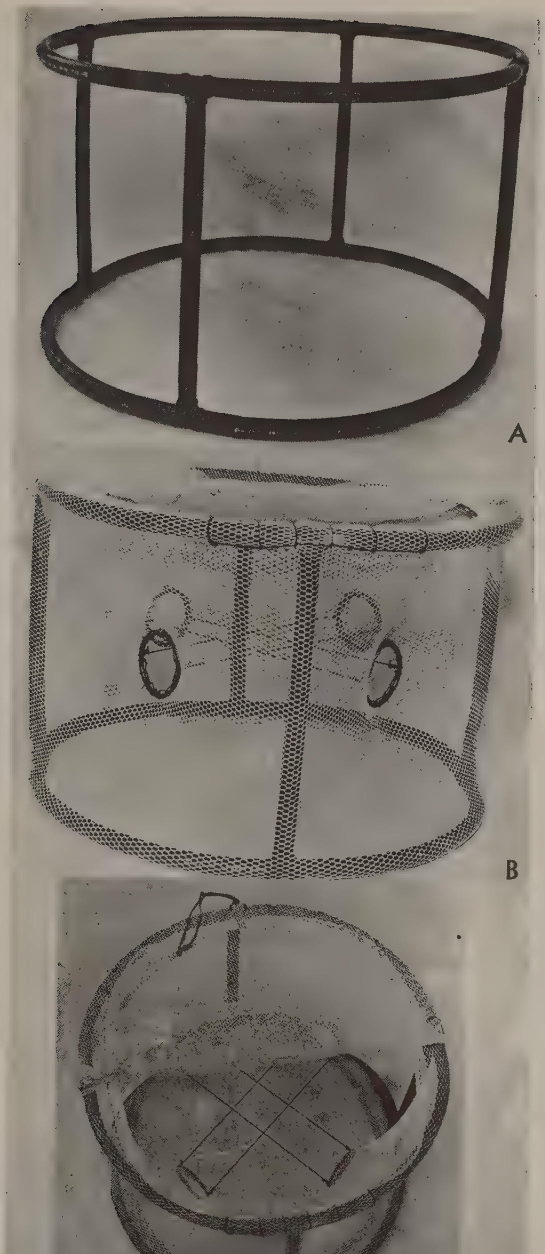

FIG. 1. Three views of shrimp pot used for experimental fishing: (A) assembled plastic pipe frame; (B) side view of pot; (C) top view; note clip attached to frame.

McBride and Barr. — J. Fish. Res. Bd. Canada

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Estuarine Nekton

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The term "nekton" belongs to a system of classification which characterizes certain aquatic organisms according to their structure and habits. The definition given in Webster's Dictionary is as succinct and accurate as any definition in the scientific literature: "The actively swimming pelagic organisms." This imparts to the nekton some characteristics unique in this system of classification of living things, for it describes a group of organisms from which all plants are excluded and which is dominated in numbers and biomass by fishes.

The nekton of estuaries is much more difficult to define. Most fishes are migratory and can tolerate wide variations in salinity. The commonly accepted definitions of an estuary, although they are not entirely in agreement, describe a restricted zone which does not encompass the entire geographic or environmental range of most nekton found in estuaries. Webster (Second Edition) describes an estuary as: "A passage, as the mouth of a river or lake, where the tide meets the river current; more commonly, a narrow arm of the sea at the lower end of a river; a frith." Or in terms of physical geography (Webster, Second Edition): "A drowned river mouth, caused by the sinking of the land near the coast." Obviously, the popular concept of an estuary has been determined on the basis of physical features. Even the biologists have accepted this concept, as illustrated by the definition given in a recent ecological text (Odum, 1959): "An estuary is a river mouth where tidal action brings about a mixing of salt and fresh water."

Most definitions of an estuary are based on two sets of criteria. On the basis of mixing of water from river and sea, an estuary should be delimited approximately by the salinity range 0 to 35 ‰. This definition is narrowed, however, by geographic restrictions which are related only remotely to the processes that create estuarine conditions. This does not necessarily fix a rigid landward boundary, but it does place an arbitrary seaward boundary on the estuary, represented by a line across a river mouth, like the mouth of the Columbia River on the west coast of North America, or across the points of land marking the entrance to a larger estuarine system like Chesapeake Bay on the Atlantic coast.

This system of classification may be suitable for sessile organisms, for their distribution is determined by average, or minimal, environmental conditions. But for actively moving, largely euryhaline animals like fishes, such a definition is not particulary useful. It is not necessary to cite literature references to call attention to the fact that many estuaries extend their influence far to sea. It is well known that the Amazon, the Mississippi, the Congo, and many other rivers influence the marine environment for many miles offshore. At the surface the horizontal gradients from fresh water to oceanic salinity usually are fairly gradual, with few sharp permanent boundaries or fronts. Indeed, in most estuaries the boundary between river water and ocean water usually is much more sharply defined with depth than along the surface. The sharpest surface salinity fronts often occur in the ocean well away from shore, under the influence of the rotation of the earth and the courses of the great permanent ocean currents.

Usually there is a surface salinity front within many estuaries near the upper limit of the estuarine zone. Its position is related to the magnitude of the river runoff and to the amplitude of the tidal cycle. In a large estuarine system like Chesapeake Bay, this front usually occurs at salinities well below 18 ‰. Massmann (1963) has described this as the "critical zone" of an estuary, rich in adults, but especially in young, of many fish species, and with abundant plankton populations. This is a fluctuating boundary, also, with respect to fixed geographic points, for its geographical position and its gradient depend on the interaction of opposing and fluctuating forces.

It is not surprising that man, a land animal, should view the ocean in the context of a system of land-based coordinates. The definitions of an estuary currently in vogue were determined largely by geographers. Yet many leading oceanographers also prefer a relatively restricted definition, like that expressed by Cameron and Pritchard (1963): "An estuary is a semi-enclosed coastal body of water having a free connection with the open sea and within which the sea-water is measurably diluted with fresh water deriving from land drainage." For many purposes this is a reasonably satisfactory view. To understand the distribution and migrations of nektonic organisms, however, the only logical point of reference is a system of oceanographic coordinates which make allowance for the fact that the estuarine environment is highly variable with respect to fixed points on land. Our present knowledge is quite inadequate to describe these coordinates precisely, but our understanding of the biology of nekton will be imperfect until we can do so.

THE NEKTONIC ESTUARY

It is interesting to consider the estuarine environment of the North American Continent as a zone bounded by salinity fronts rather than by land barriers. On the Atlantic coast the Gulf Stream immediately becomes important as the seaward boundary. A roughly triangular area bounded by the coastline, the Gulf Stream, and the Arctic seas, extending northeastward from Cape Hatteras, becomes a part of the Northwest Atlantic Estuary (Fig. 1). South of Cape Hatteras, in the South Atlantic Bight, land drainage is rather thoroughly mixed with oceanic water before it leaves the landbound estuaries and the extensive system of channels between the mainland and the coastal chain of islands. Consequently, there is no extensive offshore estuarine zone over the continental shelf in this region. North of Cape Hatteras the offshore estuarine system must be described in three dimensions, because there is a more or less horizontal front beneath the surface which is even more sharply defined. When the third dimension is brought into consideration the Northwest Atlantic Estuary becomes a vast lens of brackish water, extending to the bottom only near the shore, and underlain by a wedge of water of oceanic characteristics.

Off the Pacific coast of North America an estuarine system of even more gigantic proportions emerges under this definition. Many large rivers pour fresh water into the Bering Sea, Gulf of Alaska, and coastal areas of the Pacific Northwest. The Yukon River; the river systems draining into Bristol Bay; the many rivers of rainy Central and Southeastern Alaska; the Nass, Skeena, Fraser, and many other rivers of British Columbia; the Columbia, Sacramento, and other rivers of the United States coast all contribute to the greatest estuarine system in the world. This lens of low-salinity water extends across the entire Bering Sea and North Pacific Ocean to the shores of Kamchatka and Sakhalin where it is fed by large Asian rivers. It dips to a point southwest of the entrance of San Francisco Bay on our west coast and extends to the subarctic boundary in mid-Pacific, reaching south almost to 40° N. latitude. Under this definition the entire North Pacific Ocean, northward from 40° to 45° N. latitude, is an estuary. This has already been recognized by Tully and Barber (1960).

Parts of the Gulf of Mexico also have estuarine characteristics. The great flow of the Mississippi River system, veering to the westward as it leaves the delta under the influence of the earth's rotation, creates a lens of brackish water over much of the northwestern Gulf. The influence of the northwesterly flowing equatorial current, which carries oceanic water of relatively high salinity into the Gulf, restricts the offshore estuarine zone in the Gulf to a surprisingly narrow band, considering the great flow of the Mississippi River. It is obvious that Mississippi River water and other land drainage into the Gulf of Mexico must mix rather rapidly with oceanic water flowing into the Gulf from the Caribbean Sea and leaving again through the Strait of Florida. The relatively small influence that this great river has on the waters of the Gulf can be understood when the magnitude of the two flows is considered. The total transport through the Yucatan Channel is about 26×10^6 cubic meters per second (Sverdrup *et al.*, 1942). The average runoff into the Gulf of Mexico is about 877 cubic kilometers per year (Fleming and Elliott, 1956) or about 28×10^3 cubic meters per second, only about one-tenth of one percent of the total oceanic flow through the Gulf. A simple calculation will demonstrate that if all the freshwater runoff from the North American Continent into the Gulf were mixed thoroughly with the oceanic water entering the Gulf

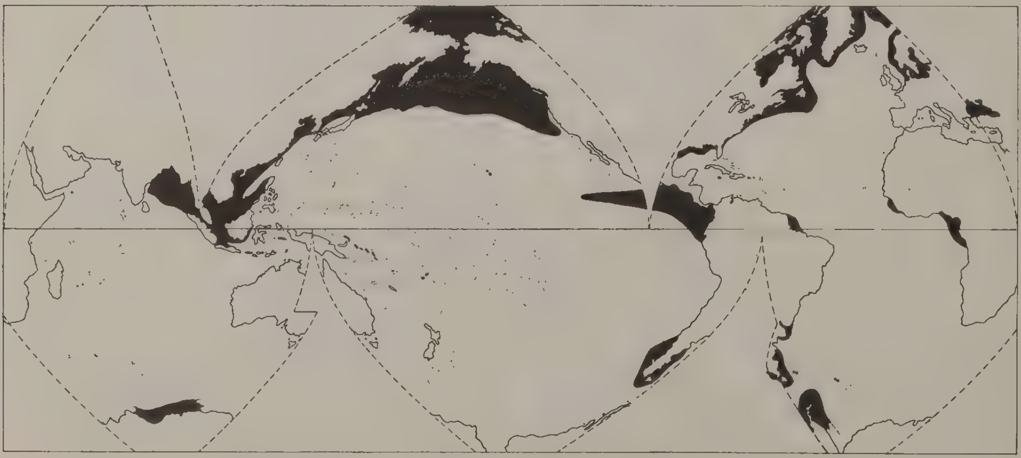

Fig. 1. Offshore estuarine zones of the world ocean bounded by the 33.5 ‰ isohaline.

through the Yucatan Channel and flowing out through the Florida Strait, it would reduce the salinity by less than 0.04‰.

The roughly triangular temperate offshore estuarine zone in the western North Atlantic is continuous with a body of subarctic estuarine water off the Labrador coast and in Hudson and James Bays. Thus, there are three major estuarine zones off the coasts of North America, the vast North Pacific zone, an extensive Northwest Atlantic zone, and a smaller zone in the northern Gulf of Mexico (Fig. 1). Contiguous with the North Pacific estuary is an extensive estuarine zone that lies in an apparently continuous band from the Okhotsk Sea along the coasts of Korea, China, and Southeastern Asia into the Bay of Bengal.

In the eastern tropical Pacific, a tongue of relatively low salinity surface water extends in a very thin layer more than a thousand miles westward from a stretch of coast off Central and South America. The surprising extent of this body of relatively low-salinity water, in a region that has no major rivers, is explained by the local climate and oceanic circulation. The fresh water that generates this offshore estuary arises principally from two sources, land drainage into the sea along at least 1,000 miles of coast from El Salvador to Ecuador, and the direct effects of precipitation. The discharge of these rivers closely follows the seasonal cycle of rainfall, with a minimum in April or May and a maximum in October or November. The flow of the Rio Tempisque, Costa Rica, in 1952 ranged from about 2,500 cubic feet per second in October to about 300 cubic feet per second in April. The average amount of fresh water contributed to the Gulf of Nicoya directly by precipitation is estimated at 5,670 cubic feet per second (Peterson, 1960). Thus, from this small gulf alone, the average contribution of fresh water to the sea probably is at least 7,000 cubic feet per second. An even greater body of low salinity water apparently originates in the Gulf of Panama (Bennett, 1963). If the entire stretch of coast from El Salvador to Ecuador contributes equivalent amounts of fresh water to the sea, the average total runoff in this region will amount to about 300,000 cubic feet per second, about half the flow of the Mississippi River. The prevailing currents in this part of the Pacific Ocean are conducive to convergence of this broadly based runoff and attenuation toward the west (Fig. 2). Peterson (1960) notes that the Gulf of Nicoya is a positive estuary, at least from May to December, for land drainage plus precipitation exceeds evaporation during this period. Moreover, at such times there is entrainment of water from below as the runoff moves seaward. Therefore, in order to maintain the salinity distribution, a compensatory flow of deeper saline water must enter the Gulf. This is the typical circulation pattern of an estuary like the subarctic region of the North Pacific (Tully and Barber, 1960). The detailed dynamics of this Central American offshore estuary is not well understood. It is likely that it varies considerably in extent in response to variations in precipitation (Bennett, 1966). Such a lack of stability would have adverse effects upon its estuarine-dependent nekton.

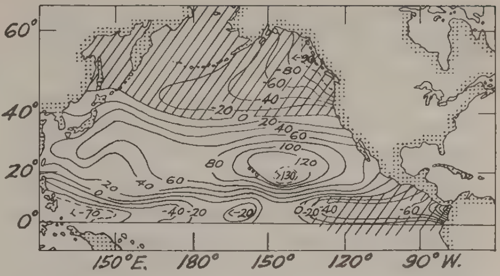

Fig. 2. Mean annual excess of evaporation over precipitation in the North Pacific Ocean (After Jacobs, 1951). The shaded zones, where precipitation exceeds evaporation, correspond closely with the two major offshore estuarine zones in the eastern Pacific (Fig. 1). The difference in the western Pacific from the pattern exhibited in Fig. 1 is related to the distribution of currents.

In the northeastern Atlantic the only extensive estuarine system includes the Baltic Sea, the southeastern part of the North Sea, and a narrow band off the Norwegian coast. In the tropical Atlantic there are three offshore estuaries, one off the mouth of the Amazon, a second off the mouth of the Niger and Congo Rivers, and a third off the West Coast of Africa from Senegal to Liberia. This third offshore estuary is not fed by any major rivers. It probably is generated by a set of circumstances similar to the climatic and oceanographic phenomena that give rise to the offshore estuarine zone in the tropical eastern Pacific off Central America. Much greater and more concentrated flows from streams like the Magdalena, Orinoco, Nile, Euphrates, Zambezi, and other major world rivers create insignificant offshore estuaries because prevailing ocean currents oppose the accumulation of fresh water at the surface, or because evaporation and mixing quickly dissipate land drainage.

The Southern Hemisphere is remarkably devoid of offshore estuarine waters. The only exceptions are a zone surrounding the southern end of South America, extending from the south coast of Chile around Tierra del Fuego and north along the southern coast of Argentina, and a band around the Antarctic Continent.

Many other estuaries exist in the world, but apparently none extends its influence far to sea. Most of the world's major river systems flow into the regions designated as offshore estuaries (Fig. 1), but there are some notable exceptions. With few exceptions the offshore estuarine zones are in regions where precipitation exceeds evaporation. Almost all major rivers which do not contribute to substantial estuarine areas enter the sea in latitudes where evaporation exceeds precipitation. These rivers include the Nile, Zambezi, and Orange Rivers in Africa; the Indus, Euphrates, Tigris, and Narbada Rivers in Asia; the Darling and Murray Rivers in Australia; and the Colorado River in North America. On the other hand, at least 35 of the 50 major world rivers flow into the zones marked as offshore estuarine zones in Figure 1.

Many of the major rivers of the world empty into the Arctic Ocean. Southward flow of this water into the North Pacific and North Atlantic must contribute substantial quantities of fresh water to the two major offshore estuaries.

Any attempt to describe the distribution and intermingling of land drainage in the ocean is quickly handicapped by a lack of information. The runoff from even the Amazon, the world's greatest drainage system, is poorly known. Studies in 1963 by scientists of the United States Geological Survey, in cooperation with the Government of Brazil, have improved our knowledge (W. B. Langbein, personal communication), but these observations were made hundreds of miles upstream, and did not include the flow of three major and many lesser tributaries. The flow of many important world rivers has never been gauged.

The general distribution of surface salinity in the world ocean is influenced primarily by precipitation, evaporation, and the effects of the major currents. From north to south, and averaged for the entire world ocean (Defant, 1961), surface salinity rises from a minimum in the Arctic regions (32.66 ‰ between 55° and 60° N. latitude) to a maximum of 35.76 ‰ between 25° and 30° N. latitude, falls to a minimum in the tropics (34.43 ‰ between 5° and 10° N. latitude), rises to a maximum between 20° and 25° S. latitude, and falls again toward Antarctica (33.96 ‰ between 50° and 55° S. latitude). This distribution corresponds very closely to the distribution of the mean sum of evaporation and precipitation, which shows excess precipitation in the Arctic, the tropics, and the Antarctic, and excess evaporation in mid-latitudes at about 20°–25° N. latitude and 20°–25° S. latitude. The offshore estuarine zones illustrated in Figure 1 fall almost entirely in the arctic or subarctic, and tropical regions, characterized by relatively low mean ocean salinities and an excess of precipitation over evaporation.

Seasonal and annual variations in land drainage are tremendous, and we know that these variations have important effects on estuarine life. We can only speculate on the biological effects of such variations in the open sea, but they must have a great influence on the movements and abundance of nekton, especially fishes. Our understanding of these relationships will require improved knowledge of the details of the earth's water budget and of the behavior of estuarine nekton.

ADAPTATIONS FOR NEKTONIC EXISTENCE

The term "nekton" identifies one group of organisms in an ecologically oriented system of classification of aquatic life based on form or habits. The benthos is composed of plants and animals attached to, or resting on, the bottom, or more or less buried in the bottom. Periphyton or aufwuchs includes organisms that are attached or cling to stems and leaves of plants or other surfaces projecting above the bottom. Plankton are usually small animals and plants which, although they may be able to swim to some extent, and can maintain or change their position between surface and bottom, essentially drift passively with the currents. Neuston includes those organisms which rest or swim on the surface. In the marine environment a simplified classification often is used: benthic life includes the benthos and periphyton; pelagic forms include the nekton, plankton, and relatively unimportant marine neuston.

To these living organisms might be added a sixth category, tripton, composed of detritus of biological origin and inorganic particulate matter. The role of this non-living suspension in the aquatic environment is not well understood (Krey, 1961). It certainly plays an important role in marine ecology, especially in the inshore estuarine environment, and its importance to estuarine nekton deserves greater attention.

The principal adaptations for truly nektonic existence are the possession of swimming organs, a smooth streamlined body, and a specific gravity reasonably close to that of the surrounding medium. Most fishes have achieved these objectives successfully by developing smooth, terete, flexible bodies covered with mucus. The bodies of most fishes can be flexed laterally but not vertically. This provides propulsive power which allows the relatively large and flexible caudal fin to move the fish forward. Many pelagic fishes are able to adjust their specific gravity by controlling the amount of gas in the swim bladder and can maintain and alter their equilibrium and direction by appropriate movements of the median and paired fins. Another important requirement for truly nektonic existence is the ability to extract oxygen at a relatively rapid rate from the surrounding water. The gills of fishes are well adapted to this mode of life, which permits active and sustained movement.

Fishes also are well adapted to withstand the rigors of the estuarine environment. Their skin, scales, and coat of mucus minimize osmotic changes associated with changes in salinity. Their capacity for active movement allows them to avoid the unfavorable effects of variations in salinity, temperature, dissolved oxygen, suspended silt, and other environmental variables. Nevertheless, the tiny young of many marine species, in which these protective mechanisms apparently are not well developed, migrate in large numbers to water of very low salinity in estuaries, where they thrive. It is generally agreed that the bony fishes originated in fresh water (Romer, 1945), and it is understandable that the young are more tolerant of low salinity. At these early stages, like young salmon, these fishes have not developed salt-secreting cells. June and Chamberlin (1958) concluded that young menhaden (*Brevoortia tyrannus*) must undergo their early development in waters of low salinity. Their experiments showed that mortality was high and development abnormal in sea water.

Most invertebrates lack this precise combination of adaptations for nektonic life. The squids are the only invertebrates that rival the fishes in this respect. Most squids have firm, terete, smooth, and relatively inflexible bodies. They swim by quite a different process, however, by a form of jet propulsion so adapted that they can move backwards as well as forwards with great speed. Squids cannot adjust to reduced salinities, however. They are important members of the oceanic nekton and enter the offshore estuary in abundance at certain places and times, but they are not typical estuarine animals.

Another molluscan group that enters the nekton occasionally is the scallop family. Normally members of the benthos, scallops are able to swim short distances by convulsive movements of the two valves of the shell. Like most of the more powerful invertebrates, however, they are prevented from adopting an exclusively nektonic existence by the presence of a heavy exoskeleton, which is necessary for attachment of the musculature.

The Crustacea are divided into two subclasses, Reptantia, the creeping forms, and Natantia, the swimmers. Some members of the Reptantia, although they do not possess true swimming organs, are able to propel themselves through the water out of contact with the bottom for limited periods. The swimming crabs, exemplified by the commercially important blue crabs of the Atlantic and Gulf coasts of the United States, have developed this capacity to a remarkable degree. This has been achieved by a modification of the fifth pair of thoracic legs to form paddle-like swimming organs, with powerful muscles. The legs and carapace are relatively smooth, slender, and light in weight, and are free of bulky spines and protuberances. By reason of these modifications, these crabs are capable of swimming off the bottom for extended periods and they perform extensive seasonal migrations.

Other Reptantia capable of swimming are the lobsters, characterized by the American lobster (*Homarus americanus*) of New England and the spiny lobsters (*Panulirus* spp.) of Florida and California. These crustaceans do not have true swimming organs, but can propel themselves with surprising agility by convulsive movements of the powerful abdomen. However, the bulky carapaces and heavy spines of *Panulirus* and the large chelipeds of *Homarus* are not conducive to extended movements off the bottom, and these occasional swimmers can hardly be termed nektonic.

Many members of the subclass Natantia are very active swimmers, although they also may crawl on, or even bury in, the substrate. Important members of this group are the shrimps, some of which, like the penaeid shrimps of the South Atlantic coast of the United States and the Gulf of Mexico, are of great commercial importance. These shrimps spawn in the ocean, but the tiny young soon congregate in the inshore estuarine areas, where they spend several months of their first year of life. The pink shrimp of southern Florida (*Penaeus duorarum*), which use the estuarine environment of the Everglades as a nursery ground, have been shown to migrate at least 120 miles from Florida Bay to the fishing grounds north of the Dry Tortugas (Costello and Allen, 1961). During this migration, and at other times, they are primarily nektonic.

All vertebrate members of the nekton other than fishes are limited in their capacity to become truly nektonic by the need to come to the surface periodically to breathe air. Whales and porpoises have been the most successful in adapting to aquatic life. They never leave the water and can remain submerged for surprisingly long periods, but they, also, must return periodically to the surface to obtain oxygen. Pinnipedes also have become well adapted to life in the water. They do need, however, to return to land to breed and some spend considerable periods resting on land. Some birds have developed remarkable capacities to dive beneath the surface and swim underwater. The rhythmic, organized mass-feeding movements of cormorants are particularly interesting (Bartholomew, 1942). Turtles and certain snakes also can swim beneath the surface for various periods. But birds, turtles, and snakes, like all air breathers, are not permanent members of the nekton.

Man is a special case. His capacity for learning to swim allows him to become a temporary member of the nekton. His ability to think, and to design, build, and operate artificial devices for catching aquatic animals makes him an important member of the nektonic community. By reason of these same abilities he possesses a tremendous capacity to modify the nektonic environment. Since he is a land-based animal, who lives mainly near rivers, lakes, and the seacoast, his influence on the estuarine environment is particularly important. Moreover, as already pointed out, his rapidly increasing numbers and evolving technology are causing him to exert an ever-increasing influence on the physical and chemical environment and on the nekton as a whole.

THE ESTUARINE ENVIRONMENT

In the enclosed or land-bound portion of the estuary, estuarine water usually can be considered as extending to the bottom. This is especially true in estuaries where strong tidal mixing usually prevents the formation of a sharp vertical salinity gradient. In some estuaries like Chesapeake Bay, however, a pronounced salinity front exists between the surface and the bottom, and the environments above and below this boundary may differ sharply. The zone of sharp transition is known as the level of no net motion (Pritchard, 1951, 1952a). Above this level the water is relatively low in salinity and has a net transport toward the sea. Below this level the water is denser and saltier, with a net transport up the estuary. This deeper water also is diluted to some extent by fresh water from the land, and its salinity is reduced gradually as it moves up the estuary.

In the offshore estuary the salinity of the deeper water usually is the same as, or not much less than, the salinity of the surface water of the open ocean

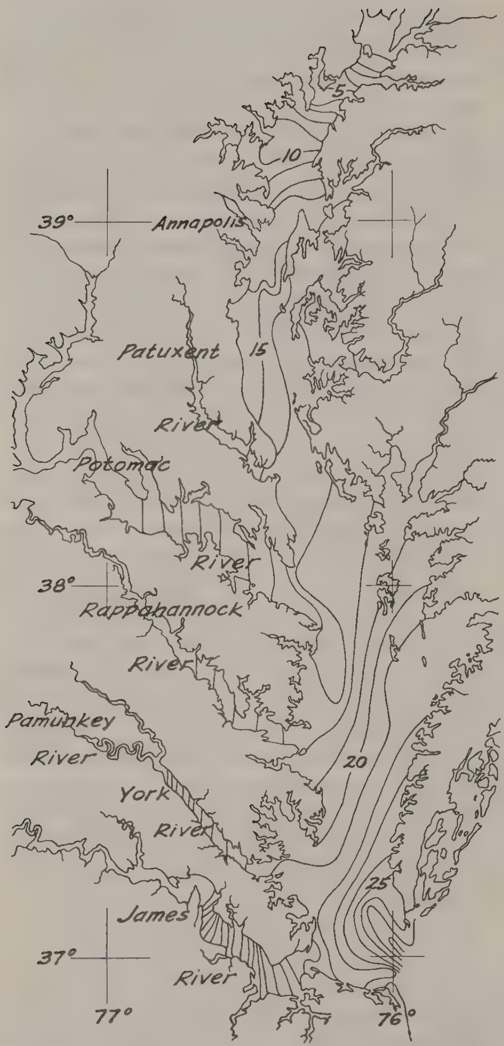

Fig. 3. Typical distribution of salinity at the surface in Chesapeake Bay.

beyond the estuarine salinity front. Details of the horizontal and vertical circulation are less well understood, but evidence is accumulating in the North Atlantic that there is an onshore transport of water near the bottom from as far out as the edge of the continental shelf, as there is in the North Pacific (Tully and Barber, 1960) and in the eastern tropical Pacific (Peterson, 1960). The outflowing surface water of reduced salinity, under the influence of the earth's rotation, is diverted to the right as it leaves the mouth of the landbound estuarine zone in the Northern Hemisphere. Hence, the surface water leaving Chesapeake Bay flows south along the coast in the direction of Cape Hatteras (Joseph *et al.,* 1960). Apparently, the Gulf Stream interposes a barrier at this point, and little if any of the low-salinity surface water passes farther south. Instead, it turns to the northward and follows the inshore edge of the Gulf Stream.

The effect of the earth's rotation is shown in the surface salinity patterns of the inshore estuaries also. In Chesapeake Bay, for example, the northerly flowing water from the sea is diverted toward the eastern side of the Bay and the southerly flowing river runoff holds to the western side. This produces a pronounced surface salinity gradient across the Bay, especially in its lower part (Fig. 3). Measurable average salinity gradients exist across the major tributaries also, with the higher salinity on the left side of the estuary looking downstream. Even the depth of the level of no net motion is affected. Careful measurements have shown that this boundary is deeper on the right side of the tributaries of the Chesapeake (Pritchard, 1952b). These general principles will apply to the structure and circulation of estuaries in other parts of the world ocean also. It should be remembered, of course, that the rotation of the earth causes the flow to veer to the right in the Northern Hemisphere and to the left south of the Equator. On the west coasts of the continents in the Northern Hemisphere, this throws river runoff to the north.

In the North Pacific the details of the structure and circulation of the offshore estuary are better understood (Dodimead *et al.,* 1963). Dodimead (1961), using the salinity structure to define major oceanographic regions in the North Pacific, described subarctic water on the basis of the presence of a well-developed halocline (Fig. 4). The boundary between subarctic and subtropic waters is identified by an almost vertical 34 ‰ isohaline extending from the surface to depths of 200 to 400 meters. This boundary, at the surface, corresponds rather closely with the northern edge of the North Pacific Drift. In the subarctic region a permanent halocline exists at a depth between 100 and 200 meters and at a salinity of about

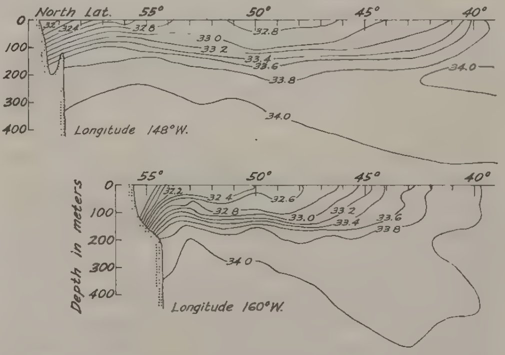

Fig. 4. Typical cross sections of the lens of low salinity water which forms the vast North Pacific offshore estuary (After Dodimead *et al.,* 1963).

33.8 ‰. As already mentioned, Tully and Barber (1960) recognized in this salinity structure the features of a simple estuarine system.

The great abundance and widespread distribution of anadromous fishes in the Northern Hemisphere, particularly in temperate and subarctic waters of the North Pacific and northwestern Atlantic, probably are related to this extensive development of oceanic estuaries. The long migrations of Pacific salmons become somewhat less of a mystery if it is conceded that they never entirely leave the influence of their home streams. Their great abundance undoubtedly can be attributed at least partially to the vast extent and high biological productivity of their offshore estuarine feeding grounds. Shad (*Alosa sapidissima*), introduced on the Pacific coast three-quarters of a century ago, are still increasing in abundance. There is good reason to believe that already this species is more abundant in the Pacific than in the Atlantic. If its oceanic feeding grounds are more extensive in the Pacific, as Figure 1 suggests, this superiority in numbers is not surprising. Striped bass (*Roccus saxatilis*) probably are prevented by temperature barriers from utilizing much of the offshore estuary in the North Pacific. Figure 1 also suggests that it would be folly to expect successful establishment of Pacific salmons or other wide-ranging anadromous species in the Southern Hemisphere in any great abundance, except perhaps along the southern coasts of Chile and Argentina.

SALINITY

At any fixed point in the inshore estuary great changes in salinity occur. These changes have a greater influence on sessile or slowly moving organisms than they do on nekton, but the nekton sometimes is affected, too. Rapid salinity changes, of course, are caused primarily by variations in rainfall or in the rate of melting of snow. The direct effects of precipitation are perhaps of little importance to nekton, but the indirect effects can be great. The major estuaries of the world receive runoff from vast areas of land. The drainage basin of the Mississippi River system, for example, covers an area of almost 1.25 million square miles. This is about 13 percent of the total area of the North American Continent. The mean flow of the Mississippi and its tributaries is about 620,000 cubic feet per second (Langbein and Harbeck, 1949) and the recorded maximum of about 1.9 million cubic feet was more than 30 times the minimum. The Amazon River system, the greatest drainage basin in the world, covers an area of about 2.7 million square miles, about 40 percent of the entire area of South America. The flow of this mighty river still has not been adequately measured, but some concept of its size may be gained from the fact that one of its major tributaries, the Rio Negro, has a volume of nearly 2.4 million cubic feet per second where it enters the main river. Thus, this tributary, which enters the Amazon 1,000 miles upstream from the sea, contributes more water than the entire Mississipi system (Office of International Scientific Affairs, 1964). Flow measurements of the Amazon proper also were made far upstream. When the contributions of tributaries like the Tocantins, Tapajos, and Xingu Rivers, which enter the Amazon lower down, are added, there is little doubt that the volume of discharge into the Atlantic Ocean under flood conditions will be at least 8 million cubic feet per second, more than four times the flow of the entire Mississippi system at flood stage. The low-water measurement of the flow of the Amazon, also made well upriver, above its confluence with several important tributaries, was about 2.5 million cubic feet per second. Variations in precipitation and runoff tend to be seasonal, but there are often sudden great changes. The passage of a major storm over the watershed can have catastrophic delayed effects on marine life in the estuary when the maximum effect of runoff from the heavy rains is felt.

TEMPERATURE

Salinity gradients are not the only important features of the estuarine environment, although it can be said that intermediate salinities are the most characteristic feature. Temperature also is an important characteristic. The level of temperature is important biologically, because respiration and osmoregulation of animals (Pearse, 1950; Pearse and Gunter, 1957) are more difficult in waters of reduced salinity, and these processes also are functions of temperature. The effects of low salinity on respiration and osmoregulation are less adverse at high temperatures. This has been accepted as the reason why southern estuaries have richer faunas than northern estuaries. The difference in variety of fish faunas between northern and southern estuaries is certainly striking. Such temperature effects also could explain the migration of many fishes out of estuaries in fall and winter.

The relatively great range of temperature in most estuaries also has important biological effects. The diurnal temperature range in a shallow estuary is relatively great (Gunter, 1945; Beaven, 1960), for such waters are quite sensitive to changes in air temperature. In the lower York River, at Gloucester Point, Virginia, for example, at a point where the water is about 5 feet deep, the bottom water temperature can vary as much as 8° F. (4.4° C.) in 24 hours (McHugh, 1959a). Relatively large vertical temperature differences also occur. In summer the surface water usually is much warmer than the deeper layers, a common characteristic of all natural bodies of water. In winter the deeper waters usually are warmer, but, more important for nektonic organisms, the temperature is relatively stable in the deeper portions of the estuary. There are important lateral gradients in estuarine water temperature also. In summer the temperature typically decreases from the upper estuary to the sea. In winter the gradient is reversed. The gradients and changes in water temperature, rather than the general level of temperature, have the greatest influence on estuarine nekton. Consequently, sudden cold waves will immobilize or kill fishes in shallow waters at temperatures that would not be lethal if the fishes were properly acclimated.

OXYGEN

In southern estuaries, especially, large variations in dissolved oxygen content of the water occur. These changes can have great effects on distribution and abundance of nekton. In Chesapeake Bay large volumes of water beneath the halocline become completely devoid of dissolved oxygen in late summer. This phenomenon affects a large area in the middle portion of the Bay and extends at times for miles up the Piankatank, Rappahannock, Potomac, and Patuxent Rivers. Its occurrence is related to the salinity structure of the water mass and the prevailing high summer temperatures. The abundant flora and fauna of the water beneath the layer of no net motion have a high oxygen demand which the natural rate of oxygen replacement is not sufficient to balance. In the absence of strong winds this deep water, once it leaves the surface outside the mouth of the Bay, can receive oxygen only by the very slow process of diffusion or advection from above. As the dissolved oxygen content of these waters approaches zero, the animals must die or move out. The only organisms that can survive are those that do not require oxygen, like anaerobic bacteria. At such times these waters contain hydrogen sulfide. Extensive mortalities of blue crabs in fishermen's pots are reported when these conditions prevail, but it is not known whether serious natural mortalities of crabs or other nekton occur. Mass fish kills occur in these areas at these and other times, but the causes are difficult to trace. There is no doubt, however, that these conditions drive nektonic forms out of the affected areas and effectively block reentry and that sometimes fishes may be trapped in restricted areas. Thus, substantial parts of Chesapeake Bay and some of its tributaries are rendered uninhabitable for fishes in late summer. The zone most seriously affected lies below the halocline or level of no net horizontal water movement, but substantial oxygen deficiencies sometimes extend to the surface. This undoubtedly affects the distribution and abundance in the Bay of densely schooling, active fishes like menhaden.

These conditions become especially acute after hurricanes deposit heavy rains over the area. Heavy runoff from the land washes large quantities of organic matter into the water, the large volumes of fresh water increase the stability of the water column, and the high summer temperatures speed up biological activity. In August, 1955, two hurricanes passed over the Chesapeake Bay area within a week of each other, with total precipitation of about 11 inches. On September 1, 1955, about ten days after the second hurricane, at a station 24 miles above the mouth of the Rappahannock River, the salinity gradient from surface to a depth of 20 feet was more than 7 ‰. The boundary between the two water masses was so sharp that the salinity at this station rose from about 10.8 ‰ at a depth of 12.5 feet to about 15.3 ‰ at 15 feet. At this time the dissolved oxygen content at 20 feet below the surface was less than 8 percent of the saturation value, and zero at 30 feet. Typical profiles of dissolved oxygen content in the Rappahannock River and Chesapeake Bay in late summer are illustrated in Figure 5.

Similar conditions undoubtedly prevail in other estuaries along the United States coast. The "jubilees" of the Gulf of Mexico are caused by similar phenomena. Brongersma-Sanders (1957) described similar conditions which caused mass fish mortalities in Walvis Bay on the southwest coast of Africa. She also cited conditions in the Sea of Azov that are similar to the phenomenon in Chesapeake Bay. Reliable quantitative estimates of fish mortalities caused by such natural oxygen deficiencies are not available. More information about the quantitative biological effects of these phenomena is needed.

OTHER FACTORS

Many other factors undoubtedly influence the distribution, abundance, and migrations of nekton in estuaries. Many authors have pointed out that nutrient-rich waters from the rivers support abundant stocks of food organisms. Others have said that these restricted, shallow waters afford a considerable degree of shelter from enemies. But it is difficult to escape the conclusion that we really know very little about the environment in which estuarine animals live. In planning "environmental" studies, we have made little progress since oceanographic research began. Measurements of temperature, salinity, dissolved oxygen, and one or two other variables usually are more or less standard practice. We measure "transparency", analyze for phosphate, and measure chlorophyll, because these are known to reflect certain aspects of biological productivity. Productivity measurements by the light and dark bottle method, and more recently by carbon-14 techniques, are frequently a part of "environmental" studies.

Odum (1959) and many other ecologists have

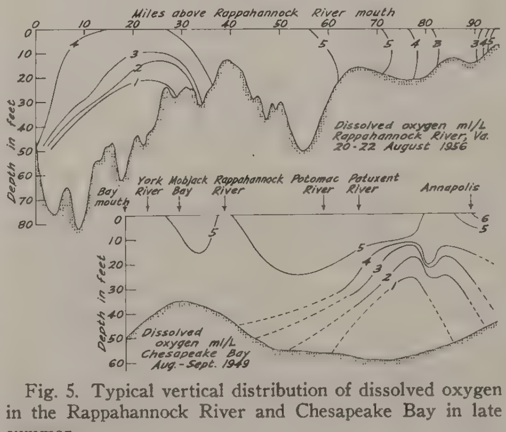

Fig. 5. Typical vertical distribution of dissolved oxygen in the Rappahannock River and Chesapeake Bay in late summer.

stressed the importance of the ecological "niche" as compared to the more general term "habitat". General measurments of environmental characteristics, like those described above, are only of limited value in describing the place where the biological community resides. By themselves these measurements do little to tell us why a variety of species can coexist in certain waters yet maintain their specific differences, or why abundance and distribution vary so greatly. We have done very little in fishery investigations to understand the microclimate in which each species lives. Yet we know from the work of Hasler (1958) and many others that fishes have acute vision, hearing, and olfactory senses by which they can orient themselves. For example, fishes apparently are able to discriminate extremely low concentrations of certain dissolved substances in the water.

Despite the fact that all biologists must have at least an elementary knowledge of the principles of ecology, a clear concept of the difference between habitat and niche has not been demonstrated in many field studies of fish distribution and abundance. The temptation is strong, when large quantities of biological observations have been made in the field, accompanied by measurements of temperature, salinity, and perhaps other characteristics of the surrounding water, to search for correlations between physical and biological variables; or, if concurrent measurements of physical and biological phenomena are not available, physical data from the same general area, collected for other purposes, have been used. Since apparent correlations often can be found by successive trials using various combinations of biological and physical data, or even with random numbers, it is not surprising that strong and apparently statistically significant correlations can be derived by trial and error from series of field observations. Now that electronic data processing facilities are so readily available, it can be expected that the search for correlations may increase. The fallacious reasoning that underlies such attempts to find relationships between variables arises from a misunderstanding of the nature of scientific hypotheses and how they should be tested. For example, it often is argued that such studies are useful in determining which observations should be continued and which should be dropped. This ignores the fact that mechanical searching for correlations can neither demonstrate nor disprove cause and effect. There is a need for more careful attention to research planning before field work begins.

We still do not know precisely what we mean by the "environment" of a nektonic individual or species. There is abundant evidence that the reactions of an organism to its environment and the influence of the environment on the organism or species are highly complex. On the other hand, at certain times unmistakable evidence of the direct and profound effects of single factors is brought forcibly to attention. Gunter (1945) has reviewed many such occurrences along the Florida and Texas coasts of the Gulf of Mexico, which sometimes affect the future success of fishing. Brongersma-Sanders (1957) has reviewed the literature on mass mortalities of nekton in estuaries caused by sudden changes in salinity, in temperature, in dissolved oxygen content, and by other natural phenomena. These catastrophic single-factor effects occur because the organism reaches the limit of its tolerance for that particular factor. But in its ordinary relations with its environment, it is virtually certain that the animal usually is integrating the effects of a relatively large number of environmental pressures, probably reacting to each in different ways according to the strengths of the other stimuli. The spectacular decline in abundance of tilefish (*Lopholatilus chamaeleonticeps*) in the northwestern North Atlantic in 1882 probably was an example of a catastrophic single-factor effect (Bigelow and Welsh, 1925). Most natural fluctuations in abundance of fishes cannot be expected to have a simple cause. Thus, it would be naive to assume that variations in survival of fishes to commercial sizes could be explained adequately in terms of variations in only one, or even several, of the many variables in the surrounding medium, even if we knew what variables are important and how they operate. This question deserves much more careful attention than it has received in the past. Field studies must be accompanied, and often preceded, by controlled laboratory experiments.

DISTRIBUTION AND ABUNDANCE OF ESTUARINE NEKTON

Our knowledge of the distribution and abundance of estuarine nekton comes almost entirely from two sources: faunal surveys and fishery investigations. The literature is extensive and it would not be practical to attempt a thorough review here. Many comprehensive studies of the fish fauna of North American coastal areas have been published. Most of these, like Jordan and Evermann (1896–1900), Clemens and Wilby (1961), Barnhart (1936), and Bigelow and Welsh (1925), describe the entire marine fish fauna of an area and not estuarine species specifically. Others, like Smith (1907), Hildebrand and Schroeder (1928), and Gunter (1941, 1945) deal with the fishes of large estuarine systems. Many of the major works are cited at appropriate places in the text, and these, together with their literature citations, provide an extensive, although by no means complete, bibliography. Many of the major faunal surveys include abundance estimates, but the best estimates of absolute abundance have been derived from the fisheries or from scientific fishery investigations. Even these are not entirely satisfactory, for, by their very nature, nektonic organisms are difficult to sample quantitatively. Some of the best estimates, although they measure only the mature segment of a population, have come from a knowledge of fecundity and counts of eggs on the spawning grounds.

According to Odum (1959), although the individual range of nekton may be great, the geographic range of a species may be less than that of many invertebrates. Nevertheless, some estuarine nektonic species have extensive geographical ranges. The Pacific herring (*Clupea pallasii*), for example, is distributed more or less continuously from the Bering Sea to San Diego Bay, a range of about 28 degrees of latitude and some 43 degrees of longitude. In a straight line between northern and southern limits, this is more than 2,000 miles. The Atlantic herring (*Clupea harengus*) also has a wide range, from the Arctic to temperate waters, and from one side of the Atlantic to the other. Within these ranges, however, both species are divided into subpopulations with more restricted ranges (Heincke, 1898; Rounsefell, 1930; Tester, 1937, 1946; McHugh, 1954).

Other nektonic estuarine fishes with wide ranges are some of the Pacific salmons, such as the red salmon (*Oncorhynchus nerka*). Alaskan red salmon from streams flowing into Bristol Bay in the Bering Sea have been caught on the high seas at least as far west as 167° E. longitude, not far from the east coast of Kamchatka, and chinook and steelhead salmon have been shown to travel even farther, from upper reaches of the Columbia River, far inland, to the vicinity of the Aleutian Islands, a distance of 2,500 miles (Hartt, 1960). Atlantic menhaden (*Brevoortia tyrannus*) occur from the Nova Scotia coast to the east coast of Florida, a range of at least 16 degrees latitude and 15 degrees longitude (Gunter and Christmas, 1960). Within this range there are apparently at least two subpopulations of *Brevoortia tyrannus* (Sutherland, 1963), but their ranges overlap considerably.

Other widespread nektonic estuarine species of the Atlantic coast of North America extend their range into the Gulf of Mexico and perhaps even farther south. Probably the most abundant of all Atlantic fishes is the bay anchovy (*Anchoa mitchilli*), which ranges from the Massachusetts coast to the Gulf. This is the most abundant species in Chesapeake Bay according to Massmann (ms and personal communication). Although this is a small anchovy, which in the adult stage can easily slip through the meshes of the trawl used by Massmann, only one fish species was caught in greater numbers in many hauls made at all seasons. Gunter (1941) also found that this anchovy is present in greater biomass than any other species in the estuarine waters of the northern part of the Gulf of Mexico. Next in abundance are the menhadens, *Brevoortia tyrannus* on the Atlantic coast and *B. patronus* and *B. gunteri* in the Gulf. Certain abundant members of the family Sciaenidae have a similar distribution. The Atlantic croaker (*Micropogon undulatus*) and the spot (*Leiostomus xanthurus*) are perhaps the most abundant members of this family among the estuarine nektonic community of the Atlantic and Gulf coasts of North America. They range from Massachusetts to Texas and support important commercial and recreational fisheries from New Jersey south. Gunter (1941) found that the mullet (*Mugil cephalus*) was the third most abundant species in Texas.

For comparison, the fish fauna of a New England estuary can be cited. Stickney (1959) listed the more important nektonic organisms of the Sheepscot Estuary in Maine. He did not give the numbers of fish caught, but it is clear that herring-like fishes and cods were important. Fewer species were represented in his collections than in collections from the Chesapeake or the Gulf, and two notable differences were evident. Firstly, the Salmonidae, which are absent farther south, were important members of the estuarine nekton in northern New England. Two species were represented, the Atlantic salmon (*Salmo salar*) and the American smelt (*Osmerus mordax*). Secondly, the croaker family, an important group in southern Atlantic and Gulf coast estuaries, was apparently rare or absent along the New England coast.

Few estuaries of the types so common along the Atlantic and Gulf coasts of the United States are found on the Pacific coast of North America. The rivers of southeastern Alaska and British Columbia empty into deep fjords or protected inshore waters created by a barrier of islands and peninsulas that extend almost continuously from Puget Sound to Skagway, Alaska. Tidal amplitudes are so great in this region that the inshore waters mix rather quickly, and the estuarine nekton is quite different from that of the Atlantic. In other parts of Alaska the major rivers flow into fjords or directly into the sea. The Columbia River and other streams of the coasts of Washington, Oregon, and California have very small inshore estuaries or flow directly into the sea. San Francisco Bay is the only really large inshore estuarine body of water on the entire west coast of North America, and it is small in comparison with Delaware and Chesapeake Bays, the North Carolina sounds, and the coastal lagoons of Texas.

The typical native estuarine fishes of the Pacific coast are anadromous. They include the Pacific salmons (*Oncorhynchus, Salmo,* and *Salvelinus*), certain smelts of the family Osmeridae, lampreys (Petromyzontidae), and sturgeons (Acipenseridae). The introduced shad (*Alosa sapidissima*) and striped bass (*Roccus saxatilis*) are well established, and both species, especially shad, may now be more abundant in the Pacific than they are in their native Atlantic waters. Shad are being caught in increasing numbers by salmon gill-net fishermen in the Fraser River (Clemens and Wilby, 1961), and the numbers ascending the fishway at Bonneville Dam on the Columbia River now are close to half a million fish a year (L. E. Perry, personal communication). The extensive offshore estuary in the North Pacific is a vast and rich feeding ground which obviously contributes to the great abundance of the Pacific salmons of the genus *Oncorhynchus,* and it, perhaps, also could support larger populations of shad.

In estuaries like San Francisco Bay, clupeioid fishes and shrimp are important members of the nekton. An interesting method of collecting nekton in San Francisco and San Diego Bays is to dip fishes off the revolving screens that protect cooling water intakes of the power and light companies. Such collections have shown that juveniles of several marine species enter these enclosed waters at times, as they do on the Atlantic coast (Herald and Simpson, 1955). The most abundant fishes, in decreasing order of total numbers caught in 248 collections from the intake in San Francisco Bay, were: surfperches (Embiotocidae, 10 species), many thousands; sculpins (Cottidae, 4 species), about 1,000; rockfishes (Scorpaenidae, 6 species), 951; herrings and anchovies (Clupeidae, Engraulidae, 3 species), 812; silversides (Atherinidae, 2 species), 387; tomcod (*Microgadus proximus*), 354; lingcod (*Ophiodon elongatus*), 322; midshipman (*Porichthys notatus*), 280; sharks and rays (Squaliformes, Rajiformes, 8 species). Several anadromous species were caught: striped bass (*Roccus saxatilis*), 168; smelts (Osmeridae, 2 anadromous, 1 marine), 19; lamprey (*Entosphenus tridentatus*), 7; and king salmon (*Oncorhynchus tshawytscha*), 2. Other groups, commonly found also in Atlantic coast estuaries, included flounders (4 species), white croaker, sticklebacks, pipefish, goby, and cusk-eel.

There is no counterpart on the Pacific coast of the mass inshore movement of larvae and young of offshore-spawning nektonic species into brackish nursery grounds that is such a striking feature of the ecology of most Atlantic coast and Gulf of Mexico estuaries. In British Columbia coastal waters, for example, Clemens and Wilby (1961) listed 272 species of fish. Only 21 of these species were described as entering the rivers, and 18 of these 21 were anadromous. The three marine species were the Pacific hake (*Merluccius productus*) which was described as a nuisance to salmon gill-net fishermen at the mouth of the Fraser River, the starry flounder (*Platichthys stellatus*), the young of which frequently move into streams, and the cockscomb prickleback (*Anoplarchus purpurescens*), a member of the family Stichaeidae, a common blenny which has been taken at the mouth of the Fraser River.

Aside from the anadromous species, which are much more abundant and important members of the estuarine community on the Pacific coast than in the Atlantic, the typical estuarine nekton of the Pacific coast is made up of the many species that inhabit the rocky intertidal zone, the fjords and channels between the coastal islands and the mainland, and the offshore estuary on the high seas. Important among these are the sharks, skates, and rays, especially the Pacific dogfish (*Squalus suckleyi*). This small, abundant shark is a great nuisance to fishermen, damaging their nets and greatly increasing their costs of operation. Many commercial and sport fishermen believe that dogfish are destructive of herring, salmon, and other species valuable to man. For these reasons, it has been proposed that a governmental bounty would encourage fishermen to destroy these pests.

The Pacific herring (*Clupea pallasii*) is an important member of the Pacific estuarine nekton. Adults spawn in the intertidal zone, where their adhesive eggs remain attached to eelgrass (*Zostera*) and other marine vegetation until hatching. The masses of eggs, exposed on the beaches and rocks at low tide, attract large numbers of gulls and other birds. They are not protected from bird predation even when covered by the tide, for they are still vulnerable to ducks and other diving birds. The young remain in the bays and channels between the islands for most of their first year of life. Several flatfish species (Order Heterosomata) perform seasonal migrations from deep to shallow water. Others spend their entire lives in relatively shallow waters. Alverson *et al.* (1964) have made the interesting observation that a species of small-mouth flounder, which feeds on small benthic molluscs, crustacea, and echinoderms, always dominates the flounder population on the inner continental shelf; whereas large-mouth flounders, which feed on zooplankton and fishes, usually predominate on the outer continental shelf and slope. Other important members of the fish fauna near shore on the Pacific coast of Canada are the seaperches (Embiotocidae), sculpins (Cottidae), gobies (Gobiidae), and kelpfishes (Clinidae). An important commercial fish of the inshore zone is the lingcod (*Ophiodon elongatus*). The Pacific cod (*Gadus macrocephalus*) makes a seasonal migration from deep to shallow water in spring.

Marine mammals are abundant members of the offshore estuarine community in the Pacific. They feed on many smaller forms of estuarine nekton, including some of commercial importance. Seals and sea lions sometimes are destructive to fishermen's nets and also damage fish in their catches. For these reasons it is commonly believed that these animals should be destroyed or that commercial uses should be developed to hold their numbers in check. Baleen whales are common in the Bering Sea and North Pacific Ocean at certain seasons, and some species come close to the coast. Sightings of baleen whales (Suborder Mystacoceti) by vessels of the United States Navy (Fleet Intelligence Center, Pacific, 1961) give some idea of the distribution of these nektonic animals in the offshore estuary of the North Pacific (Fig. 6). Most of these plankton feeders do not consume other nektonic organisms directly, although they may take in eggs and small larvae, and some species do consume fish. Their gigantic food requirements, however, may limit the food supply of other nekton at certain times and places. The gray whale (*Rhachianectes glaucus*) migrates south in winter to calving grounds in shallow lagoons along the Baja California coast. Whales have no inherent need to favor brackish over saline waters, although the movement of gray whales and humpback whales (*Megaptera nodosa*) into coastal waters at the calving season may be because it is desirable for the young to be born in shallow water (Slijper, 1962). Their presence in estuarine waters must be principally a response to the presence of abundant food. The toothed whales, and especially porpoises, may consume large quantities of fishes.

Extremely interesting seasonal successions of nekton occur in most estuaries. In far northern waters the typical cycle swings from almost complete absence of life in winter to almost an incredible abundance of

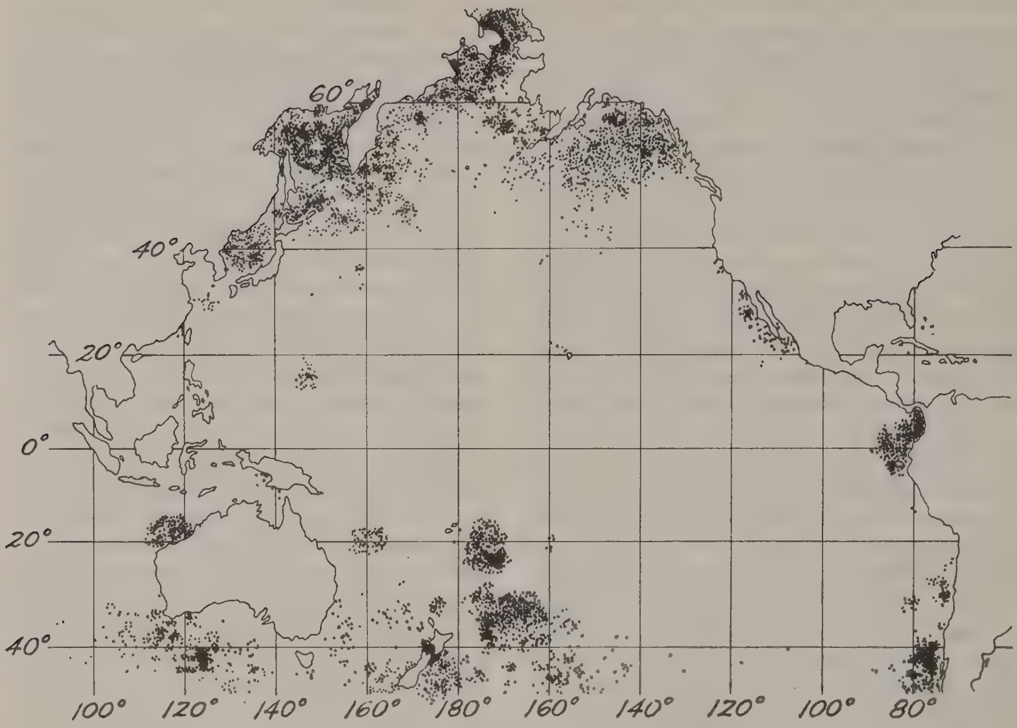

Fig. 6. Distribution of baleen whales in the Pacific Ocean, as indicated by sightings from U.S. Naval vessels.

nektonic life in spring and summer, as illustrated vividly by the following excerpt from a personal communication received in 1964 from Dr. William A. Smoker, Assistant Director of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. He was referring to Kitoi Bay on Afognak Island.

> "In April the estuary was still in the grip of a severe winter. The bay would freeze over between snowstorms and then break up and clear with rain and tidal action. Temperatures were quite low, the water clear, and nothing was observed swimming in the water. Then very rapidly as the hours of daylight increased, temperatures rose, plankton blooms occurred, herring moved in from the ocean, salmon fry and fingerlings moved in from the streams, barnacle exuviae floated all over, hexagrammids were apparent, swarms of small cottids and flounders moved around in the littoral areas, seals moved in and first chased the herring schools around and then by midsummer chased the adult salmon right up the creek mouths. A vast school of pink salmon moved in and out of a creek mouth for weeks with the tides. One could stand on the dock at 10 o'clock at night and see all sorts of nekton activity as it broke the surface of the estuary. Such animals as puffins also might be called 'nekton'. They occurred by the hundreds at Kitoi and dove and swam extensively for food, an occasional land otter would swim across the bay and dive for food, and even blooms of large jellyfish, which could be seen when the tide was slack, swimming with apparent purpose. With the decrease of daylight in late fall and winter, all of these forms disappear from the estuary and bay and again the water is cold, clear, and virtually devoid of nekton. On calm nights the skin of fresh water from the land runoff forms a layer of ice over the estuary which frequently breaks up in the tide and wind."

In temperate waters the variation in total biomass is less pronounced, but marked seasonal changes in species composition or size and age composition are common. For example, in Chesapeake Bay the smallest numbers of species are found in winter when the inshore estuarine community has been impoverished by migration of adults and most juveniles to the sea. These faunas are augmented through spring and summer by young fishes migrating downstream from nursery grounds in brackish water, and by adult fishes moving in from the ocean. The greatest diversity of species is reached late in the year (Fig. 7). Some northern forms, or deepwater species of the offshore zone, move into the Bay in winter, and some relatively non-migratory species concentrate in the chan-

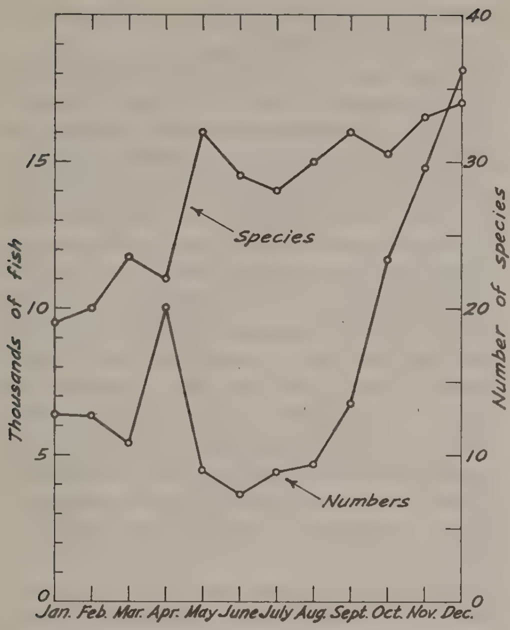

Fig. 7. Seasonal variations in average numbers of fish species and total numbers of fish caught by trawl in the York River system and Chesapeake Bay 1956 to 1959.

nels up the tributaries. Moreover, young of the year of many migratory species remain on nursery grounds in the Bay and its tributaries in winter. Thus, there is an abundant population of nekton in a temperate-zone estuary like Chesapeake Bay all the year.

The inshore estuarine environment of the Gulf of Mexico also supports a seasonal succession of species and life-history stages of nekton. The magnitude of the winter fish population in these waters can be visualized from accounts of the tremendous fish kills that occur in some winters in the northern part of the Gulf when sudden cold spells intrude (Gunter, 1945).

In temperate zone estuaries the young of fishes that utilize the brackish waters as nursery grounds grow very little until the water begins to warm in spring. Then they start adding weight and length very rapidly. As they grow, these young move slowly downstream, reaching the bays or sounds in summer and eventually moving out to the offshore estuary in late summer and fall. This is typical in the Chesapeake region of such species as the Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogon undulatus*), and spot (*Leiostomus xanthurus*). The growing season is relatively short (Fig. 8).

The first arrivals in spring, beginning to appear almost as soon as the temperature begins to rise from its February minimum, are the shad (*Alosa sapidissima*) and the river herrings (*Alosa pseudoharengus* and *A. aestivalis*). They are followed quickly by the migratory species beginning their annual inshore and northward movement (McHugh, 1960), some passing into the Bay temporarily as they proceed up the coast, others apparently taking up residence until late fall. Finally, in summer and fall, come the more temporary, but often abundant, marine visitors and stragglers, lending diversity to the rather monotonous catches of winter and spring.

These successions can be followed only partially by considering the catches by any one kind of gear. Most estuarine species seek the deeper waters of the channels in winter, but spread out into the shallower littoral areas in spring and summer. Some may be demersal at certain times, pelagic at others. Many species are most active in spring and fall and relatively inactive in midsummer and winter. Each change has a different effect on the availability of each species to each type of gear and in each part of the estuary. Thus, conclusions on relative abundance, distribution, and size and age composition of estuarine nekton must be derived from catches by various kinds of gear, integrated with a considerable amount of subjective interpretation and qualitative observation. Despite these sources of error, biologists who are experienced students of estuarine nekton are justifiably confident that their conclusions reflect the true patterns of distribution and abundance with reasonable accuracy.

Estimating Population Size

To obtain reliable quantitative estimates of the abundance of estuarine nektonic animals is difficult. Species composition, abundance, size, and age vary from low salinity to high, from shore to deep water, from surface to bottom, from season to season, and from year to year. Larger fishes usually are more successful than smaller fishes in eluding moving gear, and different species do not enter moving or fixed gear in relative proportion to their abundance. The sizes, numbers, and kinds of fish caught in a trawl, gill net, trap net, or seine vary according to mesh size,

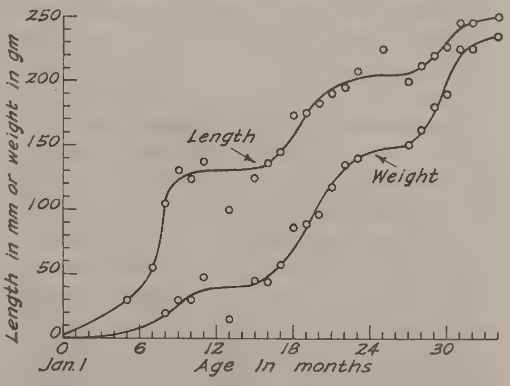

Fig. 8. Growth of menhaden (*Brevoortia tyrannus*) in Chesapeake Bay as indicated by the progression of modes in length frequency distributions of fish caught by pound nets (After McHugh *et al.*, 1960).

Table 1. Principal[1] food fishes caught by pound nets and haul seines in Virginia in 1962 (Power, 1964a).

	Pound nets		Haul seines	
Species	Thousands of pounds	Per-cent	Thousands of pounds	Per-cent
Menhaden	28,699	50.0	3,879	40.0
Alewives	21,323	37.2	1,764	18.2
Shad	1,489	2.6	17	0.2
Blue crabs	969	1.7	—	—
Spot	913	1.6	879	9.1
Gray Sea trout	776	1.4	456	4.7
Butterfish	607	1.1	467	4.8
Croaker	440	0.8	722	7.4
Striped bass	361	0.6	595	6.1

[1] Species were not included unless they made up more than two percent of the catch in one type of gear or the other.

manner in which the gear is used, and the place in the estuary in which fishing is done. These difficulties can be overcome partially by mark-and-recapture experiments, but the problems inherent in this technique are well known. They include tagging mortality or loss of tags, non-random distribution of tagged fish in time and space, and variations in mortality or behavior of tagged fish according to size, temperature of water and air, method of handling fish, or characteristics of fish behavior not yet well understood. Commercial fishing gears, which often are the most convenient way to obtain samples, operate under a variety of economic and other restrictions. They usually operate where fish are most available, they seek the most valuable species and sizes, they do not fish in certain areas and seasons, and they are subject to many other forms of bias.

Nevertheless, all methods combined can provide a wealth of useful information on the nekton. Such comprehensive studies of the fish fauna of a particular area as "Fishes of Chesapeake Bay" (Hildebrand and Schroeder, 1928) were based on observations and samples of commercial fish catches by pound nets, fyke nets, and haul seines, supplemented by scientific collections made by the research vessel "Fish Hawk." Despite the great amount of subsequent study of Chesapeake Bay fishes, this work still stands as the most useful single reference of biology and ecology of the fishes of this region. The extensive work of Gunter (1941, 1945, and many other papers) in estuaries of the Gulf of Mexico was based on collections by minnow seine, trawl, trammel net, and beach seine. Reid (1954, 1955, 1956, 1957) studied distribution and abundance of fishes in Florida and Texas estuaries using plankton nets, otter trawls, beam trawls, minnow seines, haul seines, trammel nets, dip nets, cast nets, push nets, and hook and line. Extensive studies in Chesapeake Bay by scientists of the Virginia Institute of Marine Science (various authors) and the Chesapeake Biological Laboratory (various authors) also have utilized many kinds of scientific collecting gear, and have sampled the catches of commercial and sport fishermen.

Catches by various commercial fishing gears can be compared by examining the statistical publications of the United States Bureau of Commercial Fisheries. These are not necessarily unbiased estimates of the true selectivity of these gears, however. Often, unwanted fish are discarded, and other species or sizes not acceptable for human consumption are culled out to be sold as bait (McHugh, 1960). Moreover, each type of gear is used because it is best for catching certain desirable species less available to other gears, or because it can be operated successfully in places not suited to other gears. It is interesting, however, to compare catches of different commercial gears used at the same time in the same general area. Table 1 presents a comparison of the catches of pound nets and haul seines in Virginia in 1962 (Power, 1964a). Generally, the same species were caught in both gears, and some species were taken in about equal proportions by both, but for the most part their relative importance in the catch by the two gears differed considerably. These differences were caused mainly by local and temporal differences in the distribution of these fishes.

It is interesting also to compare collections made with gears of widely different characteristics. Table 2 presents the percentage distribution, by numbers of fish, of catches made in the lower portion of Chesapeake Bay by commercial pound nets, experimental trawl, and plankton net. Conclusions as to relative abundance of the various families of fishes would be quite different if only one of these methods of collecting were used.

Figure 7 illustrates the seasonal changes in numbers of fish species and total numbers of individuals in Chesapeake Bay for the period 1956 to 1959 as indicated by catches in a trawl 30 feet wide at the mouth, with one-inch stretched mesh in the wings and three-quarter-inch stretched mesh in the cod end (Massmann, 1962). This could be interpreted as evidence that the number of species present increases from a minimum in winter (January and February)

Table 2. Relative availability of certain families of fishes caught in lower Chesapeake Bay by commercial pound nets, experimental trawl, and plankton net in the period 1956–1959. (Percentages of total numbers of fish caught by each kind of gear.)

	Pound nets	Trawl[1]	Plankton net
Engraulidae	0.4	65.5	75.7
Clupeidae	61.8	5.5	2.4
Sciaenidae	15.5	16.4	4.8
Stromateidae	18.9	3.6	0
Sparidae	2.3	2.7	0
Gadidae	+	2.6	0
Gobiidae	0	+	12.5
All other families	1.1	3.7	4.6
Totals	100.0	100.0	100.0

[1] Stations 1 to 4 (Massmann, 1962).

to a maximum in fall, and that total numbers of fish reach a minimum in summer and a maximum in late fall. The trend in numbers of species may be reasonably well depicted, for although a species may migrate seasonally into shallow waters out of reach of the net, or may otherwise become generally unavailable, it requires the capture of only a single straggler to establish the presence of that particular kind of fish. Total numbers caught, on the other hand, may be influenced by a variety of factors, among which might be migration to shallow water near shore, concentration near the surface, escapement of young through the meshes of the net, or variations in ability to elude the net with size, water temperature, and other factors. We know, for example, that menhaden of some sizes, from postlarvae to large adults, are abundant in Chesapeake Bay the year round. The sizes and ages present at any particular time, however, differ widely, and each season has its own particular pattern of distribution by size within the Bay and its tributaries. Adult menhaden are the most frequently caught fish in pound nets in the vicinity of the York River mouth (McHugh, 1960). Postlarval and young menhaden are abundant in brackish or even fresh waters of the tributaries from April to October (Massmann *et al.*, 1954). Yet menhaden were not caught in large quantities in the trawl at any time. Postlarvae and small young in the tributaries in spring and early summer are too small to be retained by the meshes of the trawl even if they were to enter the mouth of the net. Moreover, menhaden usually are most common near the surface, where they would not be available to this type of gear. Larger young and adult menhaden are too active and too near the surface to be caught in large numbers. Young croakers, which inhabit the tributaries in great numbers in late fall, winter, and spring (Haven, 1957), would also pass through the meshes of the trawl used by Massmann (1962). A number of other fishes, permanently or seasonally living near the surface (e.g., silversides), in shallow water near shore (minnows), partially buried in the bottom (cusk-eels), nocturnal (catfishes), or too small to be retained in great numbers in the cod end (killifishes), were not caught in proportion to their abundance. Failure of the trawl to catch postlarval and juvenile croakers and menhaden is sufficient to bias winter, spring, and summer catches substantially.

Insufficient data are available to estimate the total or even the relative magnitude of biomass or numbers of nekton present throughout the year in any of our inshore estuaries. In a temperate zone estuary like Chesapeake Bay large numbers of fish are certainly present at all seasons. There is little doubt that the numbers of species are least in winter and greatest in fall. Biomass also probably varies greatly with season, because very small young predominate in winter and spring and adults in summer and fall. However, there may not be a very great seasonal variation in numbers of individuals, which may be held relatively uniform by the influx of young and outmigration of adults in winter.

Fairly accurate measures of species composition, numbers of individuals, and biomass of fishes in the relatively restricted waters of small lakes or ponds have been made by killing off the entire population with rotenone or other poisons. This method has never been used on a large scale in the estuarine environment, and probably never will be a practical method of measuring abundance in such areas. Mass mortalities of nekton happen occasionally in estuaries from accidental or natural causes, and these occurrences might be used to make population estimates. Such mortalities are infrequent and usually localized when they occur in high or middle latitudes, but in semitropical or tropical waters they sometimes are sufficiently complete and widespread to suggest that fairly accurate estimates of total biomass might be made. Thus, Baughman (1947) estimated that 16 million pounds of fish died along the Texas coast in the severe cold wave of January, 1947. The red tide outbreak of 1946–1947 off the west coast of Florida killed an estimated 500 million fish, as well as turtles, bottlenose dolphin (*Tursiops truncatus*), blue crabs (*Callinectes sapidus*), and several non-nektonic species (Gunter *et al.*, 1948). Rounsefell and Nelson (1964) concluded that the effects of such mortalities on fish populations have been exaggerated. They pointed out that this kill of 500 million fish would represent only about 50 million pounds. Without denying that this is a considerable quantity of fish, they called attention to the fact that the annual menhaden catch in the Gulf of Mexico is ten times as great. Others, such as Lackey and Hynes (1955) have observed that, although fishing success is affected during and immediately after such kills, it apparently recovers rapidly, and that in the entire area affected the percentage of fish kill is low. This is probably true in general, but Gunter *et al.* (1948) stated that in the zone out to four or five miles offshore the average kill was one fish per square yard. This is equivalent to nearly 5,000 fish per acre, or 500 pounds per acre, over an extensive area of water. A yield of 500 pounds per acre per year in the sea, even in highly productive coastal waters, is considered high. Consequently, it might be concluded that the kill on the west coast of Florida in 1946–1947 could have included the total biomass of nekton in this region.

Brongersma-Sanders (1957) has summarized accounts of mass mortalities of marine animals from many different causes, but this comprehensive review of the literature contains few estimates of the biomass involved. Such estimates of the total fish fauna of an area are not often reliable, for seldom are trained observers available immediately to make accurate identifications and counts. Fish of various species and sizes vary widely in their susceptibility to environmental changes, and it is difficult to determine the precise areas of coastal water affected. Moreover, the magnitude of such kills, and their influence on the total nekton community, usually are exaggerated. Mass mortalities, therefore, even when reliable quantitative estimates are made by trained observers, usually provide only minimum estimates of total numbers or biomass.

Fishery landings from an estuarine area also provide minimum estimates of the nektonic population. These are useful estimates of the total population only when the fishery takes a large part of the entire stock. It has been estimated that about 7,500 square miles or 4.8 million acres of inshore estuarine waters fringe the United States coast of the Gulf of Mexico. In 1962, United States commercial landings of estuarine-dependent fish and shellfish from the Gulf of Mexico reached about 1.4 billion pounds. Thus, the commercial fishery yield of these inshore estuaries was about 287 pounds per acre (322 kilograms per hectare), a surprisingly large yield from natural production in the sea. When molluscs and other non-nektonic species were deducted, the total weight was reduced only slightly, and the total commercial yield of nekton from these waters in 1962 was about 282 pounds per acre (316 kilograms per hectare). This is a minimum value, for to it must be added a significant, but unknown, sport catch.

The total area of Chesapeake Bay and its estuarine tributaries is about 3,014 square nautical miles (Pritchard, 1952b), or about 2.55 million acres. Total commercial fishery landings in Maryland and Virginia in 1962 were about 521 million pounds of fish and shellfish (Power, 1964a). Subtracting oysters, clams, and other benthic resources, this figure is reduced to about 492 million pounds, or about 193 pounds per acre (216 kilograms per hectare) of nekton.

The significance of these figures is difficult to assess. Commercial fishery landings in both regions include considerable quantities of nekton caught outside the inshore portion of the estuary. About 20 percent of the nekton landed commercially in the Chesapeake Bay area in 1962 came from outside the Bay (Power, 1964a). Thus, the average commercial yield of nekton per acre from Chesapeake Bay and its estuarine tributaries in 1962 was about 155 pounds per acre. Moreover, in the Chesapeake Bay area the inshore life of some of the fish landed probably was not spent in Chesapeake Bay or its tributaries. Most of the shrimp, and substantial quantities of the fish, landed along the coast of the Gulf of Mexico come from the open Gulf. Therefore, although the nektonic species in the catches of both areas may have spent important parts of their lives in enclosed estuarine waters, their entire biomass cannot be attributed to weight added in the inshore estuary. In both regions commercial fishery yields probably should be attributed to areas broader than the area of the inshore estuaries, and the yield per acre should be adjusted downward accordingly. In the Gulf of Mexico the offshore zone affected by coastal drainage is at least four or five times as extensive as the inshore estuarine zone. If the offshore estuary also is included in computing the average yield per acre, present landings in the Gulf of Mexico are about 50 pounds per acre. Along all coasts of the United States, and some other countries, the annual yields of estuarine nekton should be augmented by unknown amounts of fish caught by sport fishermen. In the Chesapeake Bay region, for example, this sport catch might add about 10 to 20 million pounds to the catch (Richards, 1962; Shearer *et al.*, 1962).

The general conclusion to be drawn from these observations is that we cannot state exactly the standing crop or annual production in numbers and biomass of nekton in any estuary. In some parts of the world we know the species present and their relative abundance, but even these quantities are not known precisely. Attempts to compute the annual production of nekton in the inshore estuary, which is the entire estuary to most ecologists, will not produce realistic results, for most members of the estuarine nekton move freely between the inshore and the offshore estuarine environment.

FOOD CYCLES AND ENERGY EXCHANGE

Attempts to estimate the biological productivity of nekton in an estuary inevitably raise questions about feeding habits and energy transformation. The food of estuarine fishes is generally known in qualitative terms from many studies based on examination of stomach contents. It is known in quantitative terms, also, in the sense that relative volumes, weights, or numbers of the various food items usually have been described. Hildebrand and Schroeder (1928), for example, included useful information on the food of most of the 202 species of fish they listed from Chesapeake Bay. Most of the literature on this subject, however, is limited in scope and fails to deal adequately with feeding variations in time and space and their causes.

The feeding habits of most marine animals vary with age, season, and locality, and also with changing abundance of the major forage species. Thorson (1958) reviewed the literature on food of some bottom-dwelling fishes and concluded that in temperate waters they will consume an average daily ration of about five to six percent of their own body weight in summer. At lower temperatures this rate decreases significantly and feeding may cease entirely in midwinter. The seasonal cycle in feeding rate is reflected also in cyclic variations in rates of growth, as illustrated for Chesapeake Bay menhaden in Figure 8.

Hollis (1952) noted decided seasonal and regional variations in species composition of food organisms consumed by striped bass in Chesapeake Bay. He also found relatively greater numbers of full stomachs in winter and spring. These results demonstrated that estuarine fishes do not necessarily cease feeding in winter, and that their rate of feeding may not change greatly with the seasons. Metabolic rates vary with temperature, however, and striped bass, like other fishes, probably do not consume as much food in cold weather. The work of Deuel *et al.* (1944), still used by American hatcheries and commercial trout growers, demonstrated very clearly the relations between water temperature, size of fish, and food consumption for rainbow trout (*Salmo gairdnerii*). The daily food requirement of one-inch trout varied from 2.7 percent of the body weight at 36°F. (2.2°C.) to 9.9 percent at 68°F. (20°C.). For ten-inch trout the requirement in terms of body weight was much less, 0.4 percent at 36°F. and 1.7 percent at 68°F. Raney (1952), in a detailed review of the literature, found that the kinds and amounts of food taken by striped bass depend upon such factors as availability of food organisms, salinity and temperature of the water, time of day, time of year, and size and physiological condition of the bass. He concluded that striped bass generally feed upon the most abundant organisms of preferred size present in their environment, although at times they appear to exhibit food preferences when more than one desirable species is available in quantity.

No investigation, to date, has been sufficiently comprehensive to describe in adequate detail the variations in feeding in time and space of all life history stages of all important species of nekton in a natural estuarine community. Almost without exception fish food studies have been incidental to other faunistic or fishery investigations. The time, effort, and facilities necessary to do an adequate study are almost overwhelming to contemplate, but the rewards would also be great. It is undoubtedly true that, although they are by no means unselective in their feeding, marine organisms are much more efficient biological collectors than man is with his crude collecting devices. Properly conducted food studies, accompanied by controlled experiment, could provide qualitative and quantitative estimates of variations in availability and abundance and interactions between a variety of species. They could produce a tremendous amount of information on the transformation of the radiant energy that penetrates the surface of estuarine waters into proteins and other organic substances useful to man.

Fishery scientists, in their attempt to measure the effects of fishing upon estuarine resources of commercial and recreational value, have long realized that they must understand fluctuations in abundance and availability caused by natural forces as well as those caused by man. Sources of variation in mortality can be partitioned and subdivided in many ways, but at present the fishery scientist is concerned principally with the problem of separating total mortality into components related to fishing and to all other phenomena. Eventually, however, it will be necessary to subdivide still further, if the effects of these phenomena are to be understood and the knowledge is to be used to farm the sea for increased yields of desirable species. Natural mortality can be subdivided into two major categories depending on whether the causes are physical or biological. Of great importance among the biological causes are the forces of predation and competition. Yet, although predation and competition are recognized by marine ecologists as important dynamic ecological forces, the roles of which are generally much misunderstood, we have learned very little about the effects of one species upon another. It is intriguing to speculate upon the dividends that would accrue if a marine fishery research laboratory were to devote its entire research effort to such problems. Speculation upon the outcome of such studies of two important species of estuarine nekton of the Atlantic coast of North America suggests how valuable the results might be.

Menhaden as Predators and Competitors

Peck (1894), on the basis of observations of swimming rates and diameter of mouth opening of adult menhaden, concluded that these filter-feeders each could strain approximately 6.8 gallons (25.7 liters) of water per minute. Using similar assumptions, McHugh (1962) concluded that if all the adult menhaden present in the Chesapeake Bay area in a year of great abundance were within the Bay at one time they could filter all the water in the Virginia portion of the Bay and its estuarine tributaries twice in 24 hours. This is almost certainly an overestimate, for commercial menhaden landings at Chesapeake Bay ports represent catches made in the ocean as well as in the Bay, and the fishery is spread out over a five-month period during which extensive north–south migrations and movements of the fish in and out of the estuaries are taking place. Nevertheless, this startling calculation calls attention to the fact that menhaden must have profound effects upon the load of particulate matter in these estuarine waters, especially the living plankton.

Effective filter-feeders like menhaden undoubtedly ingest most, if not all, species of plankton organisms in the water that enters their mouths. The larger organisms probably are consumed in proportion to their abundance in the surrounding water. The eggs and

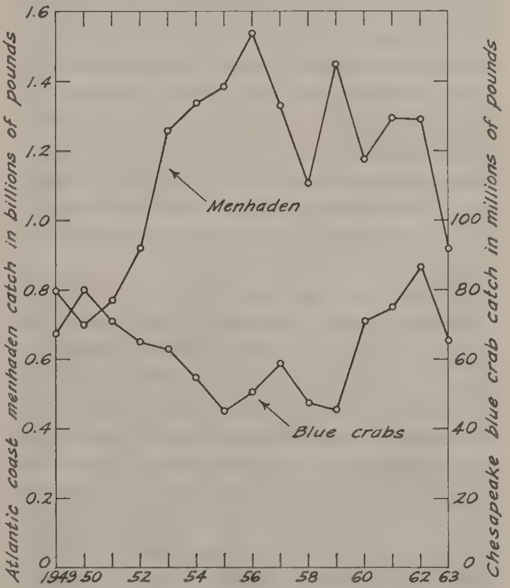

Fig. 9. Commercial catches of menhaden along the Atlantic Coast of North America, and blue crabs in Chesapeake Bay, from 1949 to 1963.

larvae of many nektonic species, therefore, are subject to predation by menhaden, and it would be interesting to know how this affects the abundance of these species. For example, in Chesapeake Bay and other estuaries of the Atlantic coast of the United States the blue crab is an important nektonic commercial species and also an important ecological element in the estuarine community. The eggs of blue crabs hatch and the larvae become temporary members of the plankton at a time and in the place where adult menhaden are most abundant. Menhaden could consume large numbers of larvae of blue crabs and other important species and could affect the future abundance of these species substantially.

The record menhaden catches of the last decade along the Atlantic coast were made possible largely by the occurrence of the unusually strong year classes of 1951 and 1958, supported by a better-than-average year class produced in 1954. The abundance of menhaden in Chesapeake Bay is roughly proportional to the middle Atlantic coast catch, if economic factors do not intervene. In the period 1949 to 1963 the smallest menhaden catches were made in 1950 and 1963, the largest in 1956 and 1959. In the same period the largest catches of blue crabs in Chesapeake Bay were made in 1950 and 1962, the smallest in 1955 and 1959 (Fig. 9). Thus, in this 15-year period, great abundance of menhaden usually was associated with low catches of blue crabs one year later, and *vice versa*.

These catch statistics, although they may be accurate representations of the total mortality of menhaden and blue crabs due to fishing, are, at best, only crude indexes of abundance. No proof of causal relationship can be inferred from this apparent inverse relationship between menhaden abundance and the future success of the blue crab fishery. Indeed, the correlation is by no means exact and it would be naive to expect that it should be, even if there were some common cause. Other factors are sure to act independently to alter the survival rates of both species. Nevertheless, it is a reasonable hypothesis that at times menhaden exert a controlling influence on blue crab abundance, and this hypothesis should be tested.

Riley (1956) estimated that the average standing crop of zooplankton in Long Island Sound was about 2 grams of organic matter per square meter of sea surface, and that the organic content was about 10 percent of the wet weight of zooplankton. Assuming that the zooplankton standing crop is about the same in Chesapeake Bay, namely, 20 grams wet weight of zooplankton per square meter, then the total standing crop in the 3014 square nautical miles of the Bay and its estuarine tributaries (Pritchard, 1952b) is about 206.8×10^9 grams. This is equivalent to about 2.5 grams of wet zooplankton per cubic meter. If an individual adult menhaden of average size in Chesapeake Bay can filter a column of water one inch in diameter at a rate of one knot it will filter about 3.9 gallons (14.8 liters) per minute (McHugh, 1962). An adult menhaden adds most of its annual growth in a 6-month period (Fig. 8). If it should maintain this filtering rate steadily for 6 months an individual fish could filter the plankton from somewhat more than a million gallons (3.785×10^6 liters) of water in 180 days. This is equal to about 3,826 cubic meters of water containing about 9,565 grams of zooplankton. In Chesapeake Bay a menhaden in its second year of life increases in weight from about 40 grams in March to about 140 grams in November (McHugh *et al.*, 1959). Even if its efficiency of conversion is only ten percent it would appear that a menhaden has a plentiful supply of food available, for at this rate it would be able to filter a volume of water containing more than nine times the amount of zooplankton necessary to provide the energy required for a growth increment of 100 grams. Moreover, this fish would have available to it also the additional microzooplankton and phytoplankton not included in this calculation, for it is probable that a menhaden is much more efficient than a No. 10 net in catching nannoplankton.

Menhaden, however, are schooling fish which must compete with each other for the available food in the surrounding water. Airplane pilots who scout menhaden for the fishing boats report that the water behind a moving school of menhaden often is clear, in marked contrast to the water ahead and to the sides. The average density of plankton available to an individual fish in a large and closely packed school must be considerably less than the average density in the surrounding water beyond the school. Moreover, although the standing crop of plankton per unit volume of water may be in excess of the needs of an individual menhaden, the rate of plankton production will limit the numbers of menhaden and other primary carnivores that a particular body of water can support.

Riley (1956) concluded that over half of the fixation of carbon by photosynthesis in Long Island Sound is consumed by respiration of phytoplankton, leaving about 205 grams of carbon per square meter of sea surface per year for consumption by animals. Some of this available energy is consumed directly by filter feeders like menhaden and molluscs, some is eaten by zooplankton which in turn is converted into useful fishery products. Since we do not know the details of this energy cycle it is not possible to compute exactly the total biomass of the end products of this biological system, but it is interesting to make some assumptions as a basis for an estimate. For example, it could be assumed that half of the available carbon is converted directly into useful resources like menhaden and half is converted into copepods which in turn are consumed by menhaden. Copepods are by far the dominant zooplankton organisms in Atlantic coast estuaries (Deevey, 1956), at least in salinities above 5‰ (Cronin *et al.*, 1962). If the efficiency of conversion of phytoplankton into copepods is 20 percent, and the efficiency of conversion of phyto- or zooplankton into menhaden is 10 percent, the total annual production of menhaden or equivalent herbivore-primary carnivores would be about 12.3 grams of carbon per square meter. According to Vinogradov (1953) about

10 percent of the living weight of a clupeoid fish is carbon. Therefore, the computed annual productivity of an estuary like Long Island Sound in terms of a fishery resource like menhaden is about 123 grams live weight per square meter per year.

It could be assumed that the biological productivity of Chesapeake Bay is similar to that observed in Long Island Sound, although this probably is a conservative estimate. Chesapeake Bay and its tidal tributaries up to the limit of saltwater intrusion would produce about 130,000 tons of secondary carnivores per year.

How does this compare with actual fishery production in the Bay? Annual landings at Chesapeake Bay ports represent catches made at distant points in the ocean, as well as from the Bay itself, but recently the official statistics have distinguished between catches from the Bay and the ocean. In 1962, for example, about 72 percent of the total commercial fishery landings in the Bay came from the inshore estuary (Power, 1964a). These inshore catches included about 253 million pounds (114,760 metric tons) of primary carnivores, mostly menhaden and other nekton, but including also about 30 million pounds (13,600 metric tons) of oyster and clam meats. The remainder, amounting to about 91 million pounds (41,280 metric tons), consisted of higher level carnivores, principally blue crabs, striped bass, croakers, catfish, spot, and weakfish. To this 91 million pounds should be added 15 million pounds (4,536 metric tons), the estimated catch of secondary or higher carnivores taken by sport fishermen. This total annual catch of secondary carnivores would be equivalent to at least one billion pounds of primary carnivores. When the annual catch of primary carnivores is added, a total catch in primary carnivore equivalents of about one and one-quarter billion pounds (571,980 metric tons) is derived, of which about 30 million pounds are benthic animals. This is about 44 percent of the estimated total annual production computed from primary production.

Fishing effort in Chesapeake Bay is relatively intense, and it would not be unreasonable to assume that the fisheries take almost 50 percent of the total annual increment of species of commercial or recreational value. An unknown proportion of the catch includes weight that was added outside the Bay, of course, for most of the catch is made up of migratory species. On the other hand, some of the net annual increment in weight of nekton is lost from the Bay by emigration. Thus, the net loss or gain may be small. However, many of the stocks of carnivorous species in Chesapeake Bay, and most of the stocks of herbivorous species, are not harvested by man.

There is good reason to believe that the transference of energy at each step in the food web is more efficient than 10 percent. Young fish are more efficient at converting food into body tissues than older fish, and most of the species of value to man that migrate into Chesapeake Bay seasonally do so in greatest proportion to their total abundance at an early age. If the calculations above had been made on the assumption that food conversion for growth is 20 percent rather than 10 percent efficient, the difference between biomass of nekton computed from primary production and the actual biomass of the catch might have been closer to reality. The obvious conclusion is that we do not know very much about biological productivity of nekton in estuaries. The principal value of the preceding speculation lies in the host of intriguing research problems it discloses.

The present catch of nekton in Chesapeake Bay averages about 125 pounds per acre (140 kg. per hectare) per year of commercial and recreational resources, a relatively high yield for a wild crop in the sea. Most yields per unit area on record from other intensive fisheries are lower than this. For example, the Sea of Azov produces about 70 pounds per acre (78.5 kg. per hectare) and the Japan Sea about 25 pounds per acre or 28 kg. per hectare (Galtsoff, 1952). The famous fisheries of the North Sea also yield only about 25 pounds per acre, and the historic Banks off Nova Scotia and New England less than 12 pounds per acre or about 13.5 kg. per hectare (Graham and Edwards, 1962). The greatest yield of nekton yet recorded from a relatively large area of the ocean is produced by the anchovy fishery of the Peru Current, which currently is yielding about 330 pounds per acre (370 kg. per hectare) to man (Schaefer, 1965).

The potential yield of primary carnivores in an estuary can be estimated in yet another way, by considering known fishery yields on intensively harvested grounds. This procedure should produce results of more practical value than estimates derived from our very sketchy knowledge of primary production and its complicated transformations. A conservative estimate of the yield of oyster grounds in Chesapeake Bay is 500 bushels of oysters in the shell every three years, or roughly 150 bushels per year. A bushel of Virginia oysters (*Crassostrea virginica*) yields about four pounds of meats. Hence, an acre of oyster bottom can produce at least 600 pounds of meats (673 kg. per hectare) per year. The area of Chesapeake Bay up to the mean limit of salt water intrusion is about 2,554,000 acres. Oysters will not survive the lowest salinities in this area, but if a suitable substrate were available perhaps 2 million acres would be capable of producing oysters, with a potential total annual yield of 1.2×10^9 pounds of meats (545×10^3 metric tons), provided that this conservative estimate of yield per unit area could be maintained over the entire Bay. This is roughly equal in weight to the present annual catch in Chesapeake Bay expressed in primary carnivore equivalents, again assuming 10 percent efficiency of conversion of primary carnivores into secondary carnivores.

A yield of 600 pounds of shellfish meats per acre per year is a conservative estimate of the potential productivity of primary carnivores in estuarine waters. Yields this large and considerably larger are not uncommon in shellfish growing areas. It appears that

Chesapeake Bay now yields the equivalent of this production per unit area of an entirely wild crop made up almost entirely of nekton, not subject to even the most primitive type of cultivation. Maximum yields in freshwater ponds in Europe exceed these figures somewhat (about 700 to 1,200 pounds per acre or 785 to 1,350 kg. per hectare). Yields in highly fertilized ponds in southeast Asia can reach much higher levels, averaging 900 to nearly 1,800 pounds per acre (1,000 to 2,000 kg. per hectare), and reaching maxima as great as two to four tons per acre (Meseck, 1962).

The land receives about the same amount of radiant energy per unit area as does the surface of the sea. Therefore, it could be expected that by applying the principles of animal husbandry to the nektonic resources of our estuaries we might obtain yields similar to those we obtain from the land. From figures given by Byerly (1962) it can be calculated that beef and hogs yield about 180 and 360 pounds per acre (200 to 400 kg. per hectare) per year, respectively. Thus, it would appear that if oysters can be considered typical of primary carnivores in an estuary like Chesapeake Bay, we are harvesting very satisfactory yields from such estuarine waters. Oysters, however, are high in water content, and 600 pounds of oysters per acre is not equivalent in protein value to 180 pounds of beef or 360 pounds of pork.

It is interesting to compare estimated plankton yields in estuarine waters with known yields from agricultural crops in the United States. Riley's studies of productivity in Long Island Sound, cited already, provided an estimated net annual production of about 1,800 pounds of carbon per acre. Assuming that the carbon content of living phytoplankton is about 5 percent of the wet weight, this means that the net annual phytoplankton production of similar estuarine areas is about 36,000 pounds per acre (over 40,000 kg. per hectare). The average annual crop of phytoplankton in Chesapeake Bay probably is somewhat greater. Average wheat yields in the United States are at least 1,000 pounds per acre per year (1,120 kg. per hectare). Average corn and wild hay crops are at least 1,800 pounds per acre (2,000 kg per hectare). Cultivated hay crops are considerably greater, producing an average of 3,000 pounds per acre (3,370 kg per hectare), and good Iowa farm land produces as much as 2,700 pounds per acre (3,000 kg per hectare) of shelled hybrid corn. The total woody material produced by Florida pine forests is at least 6,000 pounds per acre (6,750 kg per hectare) per year. Thus, the annual yield of phytoplankton in a highly productive estuary appears to be about six times the yield of higher plants on cultivated land.

Using Riley's figures, gross production of wet zooplankton in Long Island Sound is about 7,800 pounds per acre (8,740 kg per hectare) per year. Applying the arbitrary figure of 10 percent efficiency of conversion by primary carnivores, this gives about 780 pounds per acre of menhaden per year. No allowance has been made in this calculation for loss of energy by respiration of zooplankton, but this probably is more than compensated for by consumption of nannoplankton and phytoplankton by menhaden. The yield of shelled hybrid corn given above, when converted to livestock yields using the efficiency factors cited by Byerly (1962), gives estimates of about 1,000 pounds per acre of poultry, 540 pounds of pigs, or 270 pounds of cattle (1,120 to 300 kg per hectare) per year. Thus, the annual yield of menhaden in an estuary like Chesapeake Bay apparently is not greatly different from livestock yields.

Although it appears that the annual fishery harvest from Chesapeake Bay, expressed in terms of copepods or of primary carnivores like menhaden, compares favorably with yields from similar areas of cultivated land, we have virtually no measure of the efficiency of the system. We do not know whether the annual harvest represents full utilization of the annual input of energy, or under- or overutilization of the species desirable to man. Moreover, we do not understand how the various species interact with each other. It would be most useful to know what effects menhaden have upon the abundance of other nektonic or non-nektonic species which have planktonic larvae, and how the menhaden fishery influences these relationships. It would be useful also if we understood the role that menhaden and other primary carnivores play in the nutrition and biological production of striped bass and other climax predators.

Striped Bass as Predators and Competitors

The literature on feeding of striped bass has been reviewed in detail by Raney (1952) and Hollis (1952). More recent references were listed by Woodbridge and Hancock (1964). From these studies it is clear that the food is predominantly fishes, but considerable numbers of crustaceans also are taken, especially by young bass. There is no apparent preference for one food species over another, and it is reasonable to conclude on the basis of available knowledge that striped bass take nektonic species of appropriate size more or less in proportion to their abundance at the place and time of feeding. Thus, the species composition of the stomach contents varies considerably with locality and season, and also with size of bass. Striped bass feed on most other nekton in the environment and so influence the abundance of other species directly. They also compete with other secondary carnivores for the available food, and thus influence the abundance of other species indirectly.

In Chesapeake Bay in 1936 and 1937 (Hollis, 1952) at least 23 species of fish were eaten by striped bass. Those taken most frequently were the bay anchovy, spot, croaker, menhaden, river herrings, white perch, gray sea trout, and common silverside. The most important species in commercial catches in Chesapeake Bay during the five-year period 1956 to 1960 were menhaden, croaker, alewives (river herring), gray sea trout, shad, butterfish, scup, striped bass, and spot. The most abundant species in the Bay as determined by trawl hauls (Massmann, 1962) and pound net catches (McHugh, 1959b; Joseph, 1962) were bay

Table 3. Relative importance in Chesapeake Bay of major fish species in striped bass stomachs, 1936–1937; in commercial fishery landings, 1936–1940; in pound-net catches, 1958 and 1960; and in experimental trawl, 1956–1959.

Rank by weight	Striped bass stomachs	Commercial landings 1936–1940	Pound nets 1958	Pound nets 1960	Experimental trawl
1	Bay anchovy	Menhaden	Menhaden	Menhaden	Hogchoker
2	Spot	Croaker	Butterfish	Butterfish	Bay anchovy
3	Croaker	River herrings	River herrings	Gray sea trout	White perch
4	Menhaden	Gray sea trout	Thread herring	Thread herring	Silver perch
5	River herrings	Shad	Spot	Spot	Spot
6	White perch	Butterfish	Gray sea trout	Scup	Gray sea trout
7	Gray sea trout	Spot	Blue runner	River herrings	Croaker
8	Silversides	Striped bass	Bay anchovy	Silver perch	River herrings

anchovy, menhaden, butterfish, thread herring, spot, gray sea trout, river herrings, hogchoker, silver perch, white perch, and croaker. Making allowance for the fact that bay anchovy, white perch, silversides, thread herring, hogchokers, and silver perch are of little or no commercial importance, hence are not listed separately in commercial catches, this indicates a remarkable correspondence between collections made in several different ways (Table 3). It supports the conclusion that striped bass are not particularly selective in their feeding.

Hollis' (1952) study of striped bass feeding in Chesapeake Bay included more than 1,700 stomachs collected in all seasons at localities from the head of the Bay to the James River near the mouth of the Bay. However, the sampling was not adequate for analysis of variations related to size of predator or to locality. It is a major defect of this work that the size of the striped bass was not taken into consideration. The sources of variation in food and feeding habits are so diverse that it would be necessary to sample more fish at each locality, and perhaps to sample at more localities. The study should have continued for a longer period of time and should have included more physical, chemical, and biological observations. These shortcomings are not peculiar to the work cited. They can be cited for almost any study of the food of estuarine nekton that has ever been made. The interactions of striped bass with other nektonic estuarine species are diverse and complicated, as the simplified diagram in Figure 10 suggests.

Survival of striped bass and menhaden from the 1958 spawning was extremely good, producing strongly dominant year classes of both species. The causes of variations in survival of these species are not known, but it would be useful to know if this concurrent success was caused by the same factors. It is also interesting to speculate upon the influence of the large numbers of young striped bass in the estuary upon the survival of menhaden and other small nektonic animals. Could the weak year classes of 1959 to 1964 inclusive have been caused by predation by the unusually large numbers of striped bass present? Shearer *et al.* (1962) noted that striped bass of the 1958 year class in the Patuxent River Estuary did not grow appreciably from July to November, 1960. This could indicate that these predators were overrunning their food supply.

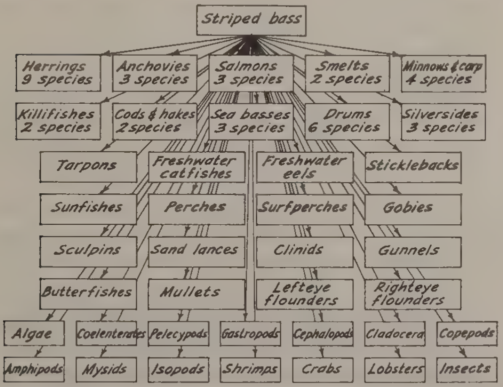
Striped bass
Herrings 9 species
Anchovies 3 species
Salmons 3 species
Smelts 2 species
Minnows & carp 4 species
Killifishes 2 species
Cods & hakes 2 species
Sea basses 3 species
Drums 6 species
Silversides 3 species
Tarpons
Freshwater catfishes
Freshwater eels
Sticklebacks
Sunfishes
Perches
Surfperches
Gobies
Sculpins
Sand lances
Clinids
Gunnels
Butterfishes
Mullets
Lefteye flounders
Righteye flounders
Algae
Coelenterates
Pelecypods
Gastropods
Cephalopods
Cladocera
Copepods
Amphipods
Mysids
Isopods
Shrimps
Crabs
Lobsters
Insects

Fig. 10. Simplified diagram of the food relationships of striped bass (*Roccus saxatilis*). Data from Raney (1952) and Hollis (1952).

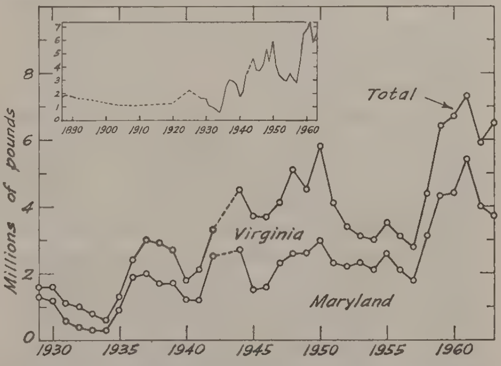

Fig. 11. Commercial catches of striped bass (*Roccus saxatilis*) in the Chesapeake Bay states since 1929. Inset shows the recorded catch of striped bass in Chesapeake Bay since 1887.

Although blue crabs are not a major food of striped bass according to the literature, they are eaten in considerable numbers at times (Hollis, 1952). Could the failure of the blue crab resource to increase in abundance in response to declining menhaden abundance in the early 1960's have been caused by increased predation by striped bass? Our ability to manage the nektonic resources of our estuarine waters for maximum sustainable yields will depend upon our ability to answer such questions.

The total annual catch of striped bass from Atlantic coast estuaries is not known. Records of the commercial catch date back to 1887, but no complete estimates of the growing sport catch are available. The commercial catch has fluctuated considerably, primarily in response to the passage of dominant year classes through the fishery. Yet, despite the gloomy conclusions drawn by Pearson (1938), Raney (1952), and others regarding the condition of the stocks and the future of the fishery, the general trend of Atlantic coast catches has been upward since 1934 (Fig. 11). It must be concluded that these authors were unduly conservative in believing that the resource was being heavily overfished, or that recent dominant year classes were the greatest on record. The late Dr. Romeo Mansueti had recognized the contradiction that existed between the recent history of striped bass catches and the pessimistic conclusions of earlier workers (Mansueti, 1961a). He had speculated that perhaps the productivity of the estuaries in terms of striped bass had been favored by the increase in nutrients produced by industrial and domestic wastes. This is an interesting and plausible hypothesis, but as Mansueti pointed out, there is no direct scientific evidence to support it. It is clear that our knowledge of the biological productivity of the striped bass resource, and the effects of fishing and other human activities upon it, is seriously deficient.

Raney (1952) stated that the sport fishery from New Jersey to Massachusetts was extraordinarily heavy, but presented no estimate of the size of the sport catch. Recent studies of sport fisheries in certain estuarine tributaries of Chesapeake Bay (Shearer *et al.*, 1962; Frisbie and Ritchie, 1963) produced estimates of 26,540 pounds of striped bass caught in the Patuxent River in 1960, and in the Potomac River 357,340 pounds in 1960 and 191,300 pounds in 1961. Several other tributaries of Chesapeake Bay are important sportfishing grounds for striped bass. Spawning is known to occur in at least 18 major rivers, from the Susquehanna in Maryland to the James in Virginia, and also in the northern end of the Bay itself (Mansueti, 1961a). It is believed that these tributaries of Chesapeake Bay are the major source of striped bass for the entire Atlantic coast fishery. Frisbie and Ritchie (1963) found that their sportfishing survey area in the Potomac River produced an average annual commercial catch of 1,150,000 pounds of striped bass in the five-year period 1958–1962 inclusive. Their complete sportfishing surveys in 1960 and 1961 gave an estimated average annual sport catch of 274,320 pounds, about 24 percent of the commercial catch. If this ratio of sport to commercial catches prevails elsewhere in Chesapeake Bay, the total catch in the record year 1961 could have been at least 9 million pounds. At 10 percent efficiency of food conversion, which may not be too conservative an estimate of efficiency for a climax predator like striped bass, this catch would equal at least 90 million pounds of primary carnivores. This is equal to about 36 pounds per acre (40 kg per hectare) over the entire area of the Bay and its estuarine tributaries. The actual yield per acre in the striped bass producing areas is considerably higher, for this species does not frequent large portions of the open Bay in any great abundance.

Man as a Predator and Competitor

Man looks upon himself as a special kind of predator and competitor of marine life. This is because, of all predatory animals, he is the only one conscious of the possible effects of his predation. The organization of human society offers mechanisms for controlling man's harvest to ensure that overfishing is prevented. This simple concept is complicated by the existence of many groups with special and often conflicting interests. Much fishery legislation has economic and social overtones which are not necessarily consistent with the principles of conservation.

To complicate matters further, the stocks of fish valuable to man are subject to wide fluctuations in abundance from natural causes. These fluctuations commonly are attributed to the effects of fishing and other human activities. Our knowledge of the causes of fluctuations in natural mortality, and the interactions of these variations with fishing mortality, is so poor that most fishery legislation and regulation are still based on opinion rather than fact, and prevailing opinion is woefully ignorant of even the elementary principles of ecology. This ignorance is particularly well demonstrated by the laws which prevail in many parts of the world restricting the capture of egg-bearing females, particularly of certain species of crustaceans which carry the developing embryos in a conspicuous external mass.

Given adequate background knowledge and an effective method of controlling total catch, man could continue to reap a large harvest from estuarine waters forever. There is little doubt that this harvest could be larger than the present harvest, although we cannot be certain how much greater. With adequate public understanding of the principles of conservation, at a level not yet attained anywhere in the world, this harvest could be obtained with less effort and less cost per pound than presently possible under existing laws. Economists who have studied the fishing industry are virtually unanimous in their belief that the only economically profitable way of managing a fishery is to create property rights to the resource by limiting entry into the fisheries (Scott, 1962). This method has been tried in some parts of the world (Gertenbach, 1962); but in some countries it has been considered unconstitutional.

Despite these complicating problems there has been no particular reason why man should consider himself unique as a predator and competitor until recently. Prior to the twentieth century, although there may have been some overfishing of limited areas or races of fish, ecological adjustments to man's predation undoubtedly had restored a balance, and most of the restrictive laws and regulations then in effect were unnecessary. This state of affairs did not change substantially until World War II wrought marked changes in human society. Even today, much of the public opinion and many of the laws and regulations governing fishing are unnecessary for conservation of the resource, although conservation often has been their stated objective. To a large extent yet, the living resources of our coastal waters have the capacity to absorb and adjust to human predation.

World War II removed the final restrictions on a scientific revolution which had been gathering momentum for a century. As a consequence, man in the post-war world is unique among animals in his fearsome ability to change the environment in which estuarine animals live. The rapidly increasing human population creates a growing need for protein, more and more of which must come from the sea. The world fishery harvest is increasing rapidly, and the wide-ranging fleets of several major fishing nations are operating wherever good catches can be made, greatly complicating the management of national fisheries. This human population growth, coupled with an unparallelled technological revolution, is changing the coastal environment, with effects upon living resources of the estuaries and coastal waters which are poorly understood but probably adverse. Thus, of all predators and competitors, man is unique, for his harvest from the sea is increasing even more rapidly than his population, and his other influences upon the environment, most of which probably are harmful rather than beneficial to the living resources, are growing even more rapidly than his catch.

Man's concern about his effects upon the resources of the ocean and their environment is as old as organized fishing. In fact, such concern arose long before significant effects appeared. The inevitable fluctuations in success of fishing caused by environmental variations stimulated restrictive laws in some countries centuries ago. The complexity of fishery regulations has increased as human society has become more complicated. Not only do various segments of the commercial fisheries attempt to limit the activity of other segments in the name of conservation, but, also, as leisure time and the funds to enjoy it have become an important part of our lives, conflicts between commercial and recreational fishing have grown. Because our knowledge of the ecology of estuarine waters is so poor, and because when man is introduced as an ecological force his social and economic habits and philosophies become important elements in the ecology of the resource, our efforts to put our imperfect knowledge to work have been confused and ineffective. The extent of this confusion and its effects can be illustrated best by an example.

For schooling fishes the purse seine has long been the most effective and cheapest kind of fishing. This gear and its method of operation are simple in principle but not generally understood by people not familiar with commercial fishing. Essentially the net is a curtain which is laid in a circle around a fish school. When the circle is complete, a cable running through rings at the lower edge of the curtain is pulled tight and the fish thereby are enclosed in a purse or bag from which they cannot escape. Large purse seines, about a third of a mile long, catch nearly all the menhaden landed along the Atlantic and Gulf of Mexico coasts of the United States. It is generally believed by people who see the large menhaden vessels and nets in operation that they catch large quantities of food of commercial or recreational value or that they compete with these fish for their favorite food. For this reason, purse seines are a constant target for restrictive legislation. The weight of scientific evidence has disproven this belief (Gunter, 1964), but in the State of Maryland opposition was so effective that purse seining was outlawed in that state in 1932. The only lasting effect has been the net loss of new wealth and revenue that would have accrued from an investment of capital in the menhaden fishery, and probably a corresponding gain by the State of Virginia and its citizens. Although conclusive scientific proof is lacking, circumstantial evidence leads to the conclusion that Maryland's gain in increased catches of striped bass or other carnivores was nil.

To the ecologist these unproven beliefs fail to recognize the complexity of interrelationships between marine animals and their environment. Menhaden are not obvious predators upon other resources valuable to man, yet they could consume large numbers of larvae of other species, as already noted. Thus, it would be just as logical to approve menhaden fishing on the ground that it will reduce predation upon blue crabs, oysters, or many species of fish, as to condemn it for its supposed predation on, and competition with, striped bass or other valuable fishes. At our present level of knowledge it is necessary, in rebuttal to unfounded proposals to restrict menhaden fishing operations, to present arguments based upon equally unfounded speculation. This is necessary in order to emphasize the complexity of ecological relationships and to prevent undue restriction of fishing operations, but it is a poor substitute for demonstrated knowledge. This emphasizes the importance of broad ecological studies of the estuarine environment, to identify the opposing forces that determine growth and survival rates of estuarine nekton, and clarify the roles of the various factors, natural and man-made, which determine the size of the maximum sustainable yield.

THE ESTUARINE NEKTON

Having defined the nektonic estuary and having discussed in general terms the kinds of animals that inhabit this environment, it is appropriate now to consider in detail the nekton of an important estuary, its distribution, and its movements. Sverdrup *et al.* (1942) have said that the nekton as a whole includes most of the adult squids, fishes, whales, and some others: marine animals that are able to migrate over considerable distances. Considering the narrow definition of an estuary for the moment, it is clear that estuarine nekton consists almost entirely of fishes. Cephalopods are not abundant in waters of greatly reduced salinity. With few exceptions, cetaceans and pinnipeds are casual visitors. The truly indigenous nekton of an inshore estuary along the middle and south Atlantic coasts of the United States and in the northern part of the Gulf of Mexico, regions of greatest estuarine development along North American shores, consists of only a few fish species, some of which have habits which scarcely qualify them as nekton and which, as a group, do not make up a very large part of the total nektonic biomass. Indeed, even when an estuarine system as large as Chesapeake Bay is considered, if the inner limit is taken as the upper limit of intrusion of sea salt and the outer limit as a line between Cape Charles and Cape Henry, few nektonic animals remain permanently within this zone. Even nektonic invertebrates like the blue crab (*Callinectes sapidus*) and the penaeid shrimps do not qualify as estuarine nekton under this restrictive definition. Moreover, if these inhabitants of the landbound estuary are considered only in relation to this temporary segment of their environment, it is virtually impossible to understand their dynamic ecological relationships with their entire environment.

Hedgpeth (1957) has reviewed various classifications of estuarine organisms based upon their salinity tolerances. None of these is entirely satisfactory for fishes, although the system of Day (1951) is reasonably adequate. It is convenient to develop a somewhat different classification for the purposes of the present discussion, as follows:

1. Freshwater fishes that occasionally enter brackish waters.
2. Truly estuarine species, which spend their entire lives in the estuary.
3. Anadromous and catadromous species.
4. Marine species which pay regular seasonal visits to the estuary, usually as adults.
5. Marine species which use the estuary primarily as a nursery ground, usually spawning and spending much of their adult life at sea, but often returning seasonally to the estuary.
6. Adventitious visitors, which appear irregularly and have no apparent estuarine requirements.

With the exception of Hudson and James Bays, Chesapeake Bay is the largest inshore estuary of the North American coast. Its hydrography and biology are reasonably well known. The two-layered circulation of the typical positive estuary is well developed, with substantial and permanent flows of fresh water toward the ocean at the surface and salt water into the estuary at greater depth. Various discussions of the relations between physical and biological phenomena in Chesapeake Bay have been published (Pritchard, 1951; Massmann and Pacheco, 1957; Schwartz, 1963), but no thorough analysis and interpretation of all available data have been made. Such an analysis is beyond the scope of this paper, but a review of the nekton in terms of the classification presented above will serve as an example of the nekton of an important and fairly typical inshore estuary. It also may stimulate further analysis of existing information and perhaps suggest subjects for additional useful research.

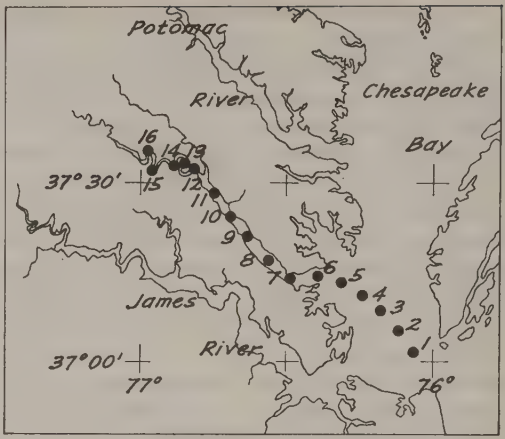

Fig. 12. Locations and serial numbers of trawl stations in the York River system and Chesapeake Bay (After Massmann, 1962).

Probably the most detailed survey of distribution and abundance of Chesapeake Bay fishes was made in the York River system and the region between the York River mouth and the entrance to Chesapeake Bay by Massmann (1962). He made standard trawl hauls at a series of 16 stations spaced at approximately five-mile intervals from fresh water in the Pamunkey River, a tributary of the York, to the mouth of Chesapeake Bay (Fig. 12). With few omissions, the trawl was fished each month at each station from April, 1956, to November, 1959, inclusive. These data have never been analyzed in detail, but the tabulated data in the report cited above, and a more detailed unpublished manuscript which the author has kindly allowed me to examine, contain a wealth of interesting material. Further analysis was hampered by the fact that the data were grouped into four river sections, each including four stations. The catches of individual stations were not available without reference to the original data.

Seasonal and incidental variations in bottom salinity values in adjacent sections of the transect overlapped considerably during the period of the survey, but the four zones generally fitted the classification outlined by Hedgpeth (1951). Hedgpeth defined the freshwater zone as that environment having a salinity less than 0.5 ‰. Stations 13 to 16 in Massmann's

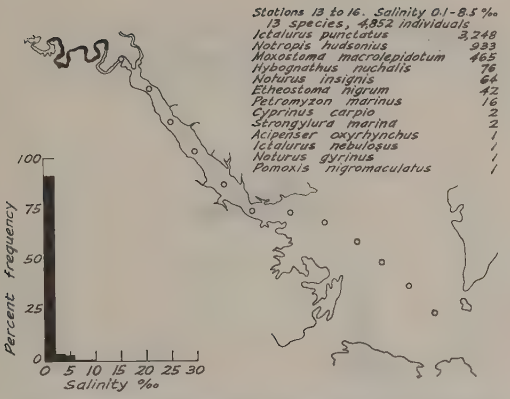
Stations 13 to 16. Salinity 0.1-8.5 ‰
13 species, 4,852 individuals
Ictalurus punctatus 3,248
Notropis hudsonius 933
Moxostoma macrolepidotum 465
Hybognathus nuchalis 76
Noturus insignis 64
Etheostoma nigrum 42
Petromyzon marinus 16
Cyprinus carpio 2
Strongylura marina 2
Acipenser oxyrhynchus 1
Ictalurus nebulosus 1
Noturus gyrinus 1
Pomoxis nigromaculatus 1
Percent frequency
100
75
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 13. Species caught by trawling in the Pamunkey River (Stations 13 to 16), but not taken in other sections of the transect.

transect, grouped as the Pamunkey River stations, fell on the average within the freshwater ecological zone (Fig. 12). Station 13 actually would more logically be classed as oligohaline (average salinity 0.5 to 3 ‰), for the average bottom salinities at this station usually fell within this range. Stations 9 to 12, the upper York River stations, included the oligohaline and mesohaline (average salinity 3 to 16.5 ‰) ecological zones. The lower York River, including Stations 5 to 8, and the Bay, Stations 1 to 4, were included within the polyhaline zone (average salinity 16.5 to 30 ‰). The marine zone (salinity greater than 30 ‰) often encroached upon the lower end of the transect, sometimes extending into the Bay as far as Stations 3 or 4 (Fig. 12). The freshwater zone usually included Stations 14 to 16, and occasionally extended downriver at least to Station 12. As pointed out already, collections by one kind of gear do not give an unbiased picture of the nekton of a region. Hence, the discussion will be supplemented, where necessary, by reference to other collections by other types of gear.

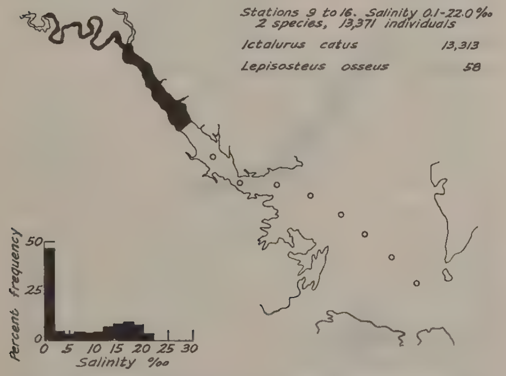
Stations 9 to 16. Salinity 0.1-22.0 ‰
2 species, 13,371 individuals
Ictalurus catus 13,313
Lepisosteus osseus 58
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 14. Species caught by trawling in the Pamunkey River and upper York Rivers (Stations 9 to 16), but not taken in other sections of the transect.

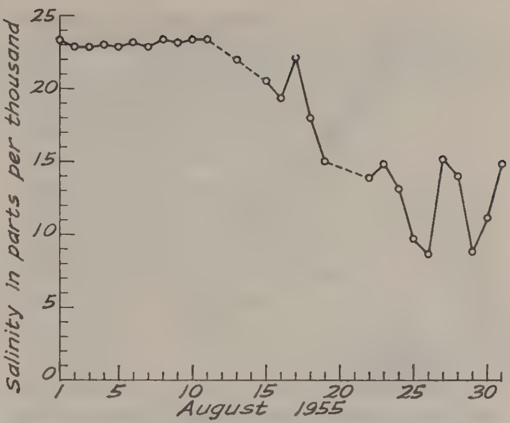

Fig. 15. Variations in salinity at the surface at Gloucester Point in the York River before, during, and after passage of a hurricane.

Freshwater Fishes That Enter Brackish Water

This category includes fishes that cannot be called estuarine species, for their tolerance for salt water is not great. Occasionally, however, they may stray far beyond the areas in which normally they might be expected to be found, as illustrated by the occurrence of a bluegill (*Lepomis macrochirus*) in a sample from a pound net catch in Chesapeake Bay at the mouth of the York River on May 20, 1958 (McHugh, 1960). This demonstrates the ecological impracticability of an estuarine definition based on geographic coordinates. This was a period of heavy runoff in the Chesapeake Bay region. The salinity of the water of the York River, six miles upstream from Chesapeake Bay, at this time was only about 12 ‰, and the salinity at the pound net site could not have been more than one or two parts per thousand greater, probably not above 15 ‰. Consequently, the landward boundary of the estuary at this time must have been displaced about 25 miles seaward.

Species confined exclusively to the Pamunkey River (Stations 13–16) numbered 13. The area under discussion, the species caught, and the frequency distribution of salinities at the bottom during these trawl hauls are illustrated in Figure 13. Ten of the 13 species were freshwater fishes. The other three species accounted for only 19 individual fish of the total catch of 4,852. Two of these three were anadromous species which obviously are not confined to this section of the York River system or the areas upstream from it. Of these, the sea lamprey (*Petromyzon marinus*) is not readily caught in trawls, and the Atlantic sturgeon (*Acipenser oxyrhynchus*) is extremely scarce.

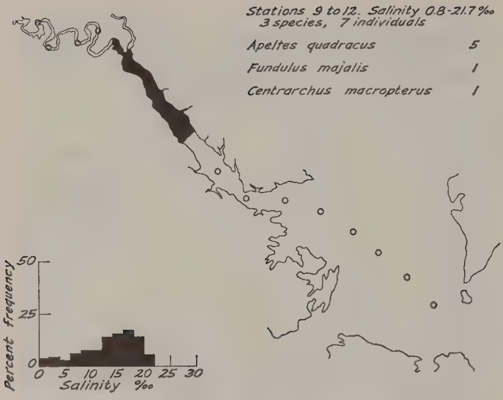
Stations 9 to 12. Salinity 0.8-21.7 ‰
3 species, 7 individuals
Apeltes quadracus 5
Fundulus majalis 1
Centrarchus macropterus 1
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 16. Species caught by trawling in the upper York River (Stations 9 to 12), but not taken in other sections of the transect.

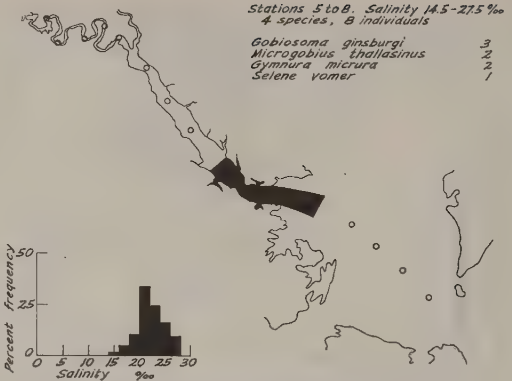
Stations 5 to 8. Salinity 14.5-27.5 ‰
4 species, 8 individuals
Gobiosoma ginsburgi 3
Microgobius thallasinus 2
Gymnura micrura 2
Selene vomer 1
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 17. Species caught by trawling in the lower York River (Stations 5 to 8), but not taken in other sections of the transect.

The third, the Atlantic needlefish (*Strongylura marina*), is a slender euryhaline surface swimmer which would not be expected to be available in large numbers to a bottom trawl. It can be concluded that the three species that did not belong exclusively to fresh water are not endemic to the freshwater and oligohaline zones, as the other ten species apparently were. These ten were all freshwater forms, native to the Pamunkey River, which entered the upper end of the estuary temporarily.

Two additional species taken in the Pamunkey River were captured in the upper York River as well (Stations 9–16). Of the total catch of 13,371 fish taken in this section (Fig. 14), 13,313 were white catfish (*Ictalurus catus*), a freshwater species with a somewhat greater tolerance for brackish water than those freshwater species caught only in the Pamunkey. The other 58 fish were longnose gar (*Lepisosteus osseus*), another salt-tolerant freshwater form.

Thus, all fish taken exclusively in the Pamunkey River or common to this section and the upper York, with the exception of two anadromous species and one euryhaline marine species not readily available to the trawl, belonged to freshwater species, some of which ventured into the mesohaline portion of the estuary where salinities usually did not exceed 16.5 ‰.

During these extensive trawl surveys no freshwater fishes were caught in the lower York River (Stations 5–8) or in the Bay (Stations 1–4). These results suggest that freshwater fishes in the York River system do not stray in significant numbers beyond the point in the river where the salinity usually exceeds 16 to 18 ‰. This does not mean that freshwater fishes never enter the lower York River or the Bay, for during freshets unusually low salinities may prevail in all parts of the Chesapeake estuarine system. The capture of a bluegill in a pound net in the Bay during such a freshet has been cited already. Variations in salinity at Gloucester Point, near the mouth of the York River, following passage of two hurricanes over the area, are illustrated in Figure 15. Such a variation in salinity represents a shifting of oceanographic coordinates of the order of 35 or 40 miles.

Truly Estuarine Species

Species of fish which never enter fresh water and never pass beyond the entrance to Chesapeake Bay could be termed endemic fishes of the inshore estuary. Two sections of the trawl transect can be examined to determine whether any species caught meets this requirement: the upper York River (Stations 9–12) and the lower York (Stations 5–8). If any species was taken exclusively in either of these sections or in both sections, but not beyond, that species might be considered a fish of the inshore estuary.

In the upper York only, three species were caught (Fig. 16). The total catch of fishes taken exclusively in this zone was only seven individuals. The four-

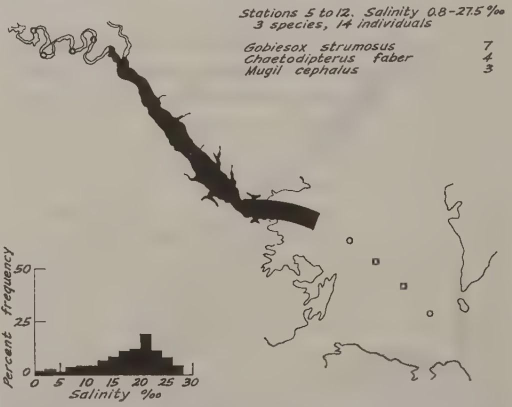
Stations 5 to 12. Salinity 0.8-27.5 ‰
3 species, 14 individuals
Gobiesox strumosus 7
Chaetodipterus faber 4
Mugil cephalus 3
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 18. Species caught by trawling in the upper and lower York River (Stations 5 to 12), but not caught in other sections of the transect.

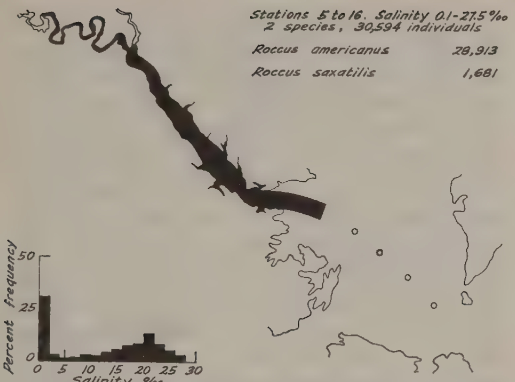

Fig. 19. Species caught by trawling in the York and Pamunkey Rivers (Stations 5 to 16), but not taken in Chesapeake Bay.

spine stickleback (*Apeltes quadracus*) and the striped killifish (*Fundulus majalis*) are abundant small fishes of shallow waters which would easily pass through the meshes of the net, and which normally do not frequent the deeper waters of the river channel. The distribution of both species is much more extensive than these small catches would suggest. The stickleback enters fresh water, and, thus, is not strictly an estuarine species. The killifish, on the other hand, may well be an endemic estuarine form, for there are no records of it from fresh water or from the sea in the Chesapeake region. It is a widespread inhabitant of inshore estuaries from Massachusetts to Florida. The third species, the flier (*Centrarchus macropterus*) belongs to an important family of freshwater fishes, some members of which occasionally stray into brackish waters. Its absence in catches from the Pamunkey River simply confirms its rarity in brackish water. Thus, the trawl catches provided no evidence that any truly estuarine species were limited in their distribution to the upper York River.

Species caught only in the lower York were represented by equally small numbers of fish. Only eight individual fish, belonging to four species, were taken (Fig. 17). Two of these, the smooth butterfly ray (*Gymnura micrura*) and the lookdown (*Selene vomer*), are marine species which enter the estuary in summer. Their occurrence exclusively in this section of the transect is indicative only of their rarity in trawl collections. None of the elasmobranch fishes was caught in great numbers in any part of the survey area, although they are relatively abundant in the lower part of the Bay in summer. Like most carangid fishes, the lookdown is an active swimmer of the upper water levels, not easily caught in a bottom trawl. The two gobies (*Gobiosoma ginsburgi* and *Microgobius thalassinus*) are small shore-dwellers which normally would not be in the deeper waters sampled by the trawl. Both have wider ranges in the Chesapeake region than these trawl catches indicate. There is not sufficient evidence in the trawl collections to suggest that either goby is entirely a fish of the inshore estuary. Thus, the sparse collections of fishes caught only in the lower York River provide no evidence that any species resides exclusively in this section of the river.

Species caught in the upper and lower York River (Stations 5–12), but not beyond, were equally poorly represented (Fig. 18). Only 14 individuals, belonging to three species, were taken. The skilletfish (*Gobiesox strumosus*), although it is not restricted to this limited section of the estuary, is fairly certainly endemic to the inshore estuary in the Chesapeake region. Hildebrand and Schroeder (1928) found it in greatest abundance from the York River to the vicinity of Annapolis. Its small size, shallow-water habitat, and habit of clinging to shells and other firm surfaces, explain the small catches in the trawl. Its habits are not conducive to life off open ocean shores, and it has not been reported from fresh water. This probably is one of the few truly endemic estuarine fish species of Chesapeake Bay and other Atlantic inshore estuaries, but its sedentary habits scarcely qualify it as a truly nektonic animal. The Atlantic spadefish (*Chaetodipterus faber*) and the striped mullet (*Mugil cephalus*) are seasonal visitors to the Bay. Their occurrence only in catches from this restricted zone must be attributed to chance. Both are active swimmers which enter the Bay from the ocean regularly in summer, sometimes in great numbers, and they are able to evade a slow-moving trawl with ease.

Anadromous and Catadromous Species

Adequate collecting along the entire transect (Stations 1–16) should take representatives of all anadromous and catadromous species native to the Chesapeake Bay estuarine system at all stations, unless for some reason certain species or life history stages are not available to the trawl. Thus, the collections of anadromous and catadromous species should provide a test of the adequacy of the gear and the design of the sampling program.

The record of catches in the York and Pamunkey Rivers (Stations 5–16) shows that only two species were taken in all sections of this transect, but not in the Bay (Fig. 19). Both these species are anadromous. The white perch (*Roccus americanus*) was very abundant in this section of the estuary. Mansueti (1961c) and Woolcott (1962) have suggested that several more or less independent populations of this species inhabit various tributaries of Chesapeake Bay. Its absence from trawl hauls in the Bay, despite its relatively great abundance in catches in all parts of the York River system, and its absence from pound net catches off the mouth of the York River and in other parts of the lower Bay (McHugh, 1960; Joseph, 1962), appear to confirm this conclusion. Mansueti (1961c) concluded that the population in the Patuxent River was essentially self-contained, and Massmann's trawl collections suggest that this may be true for

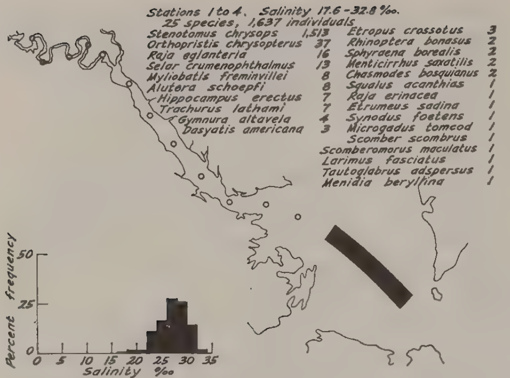
Stations 1 to 4. Salinity 17.6-32.8 ‰.
25 species, 1,637 individuals
Stenotomus chrysops 1,513
Orthopristis chrysopterus 37
Raja eglanteria 16
Selar crumenophthalmus 13
Myliobatis freminvillei 8
Alutera schoepfi 8
Hippocampus erectus 7
Trachurus lathami 7
Gymnura altavela 4
Dasyatis americana 3
Etropus crossotus 3
Rhinoptera bonasus 2
Sphyraena borealis 2
Menticirrhus saxatilis 2
Chasmodes bosquianus 2
Squalus acanthias 1
Raja erinacea 1
Etrumeus sadina 1
Synodus foetens 1
Microgadus tomcod 1
Scomber scombrus 1
Scomberomorus maculatus 1
Larimus fasciatus 1
Tautoglabrus adspersus 1
Menidia beryllina 1
Percent frequency
50
25
0
0 5 10 15 20 25 30 35
Salinity ‰

Fig. 20. Species caught by trawling in Chesapeake Bay (Stations 1 to 4), but not taken in the York or Pamunkey Rivers.

the York River also. Opposed to this conclusion is the fact that Hildebrand and Schroeder (1928) collected white perch at Cape Charles and Cape Henry, just inside the Bay entrance, and that Mansueti (1961c) found that some fish from the Patuxent River population sometimes moved into the Bay. Moreover, the striped bass (*Roccus saxatilis*), which is known to migrate from Chesapeake Bay to such distant waters as off the coast of Maine (Raney *et al.*, 1954; Mansueti, 1961b; Massmann and Pacheco, 1961), was also taken in trawl hauls in the York River system, but not at the four stations in the Bay. Thus, absence of white perch from trawl catches in the Bay cannot be taken as conclusive evidence that a race of this species is confined entirely to the York River system.

The largest striped bass caught was about 300 mm in fork length, which according to Mansueti's (1961b) illustration of the length-weight relationship would weigh about 450 gm and would be not more than three or four years old. Various authors agree that during the first few years of life striped bass do not move far from their native river. Therefore, the absence of striped bass from trawl catches in the Bay means only that the trawl does not capture the larger fish prevalent in these waters. This could also mean that larger and older white perch might also move from the river into the Bay, where they also might escape the trawl. The largest white perch caught in the trawl, however, were 290 mm in fork length, which, according to data presented by Mansueti (1961c) would weigh about 900 gm. This is close to the maximum size for this species cited by Hildebrand and Schroeder (1928) and Mansueti (1961c). It is fairly obvious that there was less bias in sampling white perch with the trawl; and from the weight of other evidence, it can be concluded that white perch probably do not move from the mouth of the York River into the Bay in great numbers. There is absolutely no evidence that this species leaves the mouth of the Bay to enter the ocean.

Seven other anadromous and one catadromous species were caught during the trawl survey. Two of these, as mentioned in a previous section, were taken only in the Pamunkey River. Of these two, the sea lamprey (*Petromyzon marinus*) is not abundant in the Chesapeake region (Mansueti, 1962b) and its small ammocoete larvae and migrating young are not likely to be caught in a trawl. The relative scarcity of adults, their shape, and their brief sojourn in the inshore estuary probably explain the small catch (only 16 young individuals in nearly 4 years) and their apparent absence at most stations. The second, the sturgeon (*Acipenser oxyrhynchus*), is becoming increasingly rare in Chesapeake Bay, as elsewhere in the world, and it is not surprising that only one young fish was caught. Raney and Massmann (1953) reported that the sturgeon is rarely seen in the Pamunkey River.

The hickory shad (*Alosa mediocris*) was caught in small numbers in the Bay and the York River (Stations 1–12), but not in the Pamunkey. It is the least abundant of the river herrings in the Chesapeake region and, until recently, the opinion was held by many authors that it does not spawn in fresh water. Mansueti (1962c) reviewed the life history of this species and presented evidence that it does spawn in fresh water in the Patuxent River, Maryland. He suggested that the consistently poor catches of young hickory shad meant that this species is particularly adept at avoiding fishing gear. The capture of only 21 hickory shad in nearly four years of trawling, and its absence in trawl catches in the Pamunkey River, is consistent with the experience of other investigators. It is interesting, however, that Raney and Massmann (1953) presented evidence that this species spawns in fresh water in the Pamunkey River. They also reported a catch of 91 young in two 15-minute hauls with a surface trawl (Massmann *et al.*, 1952) in the same section of the river as the bottom trawl surveys of 1956–59. If the young remain near the

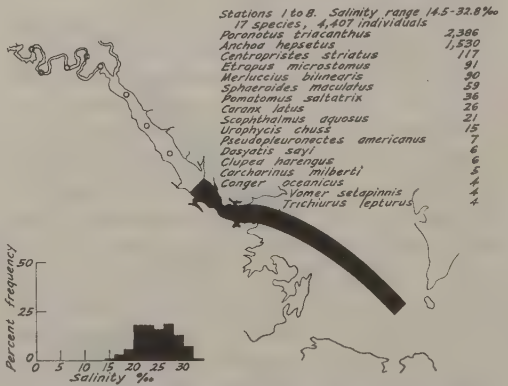
Stations 1 to 8. Salinity range 14.5-32.8‰
17 species, 4,407 individuals
Poronotus triacanthus 2,386
Anchoa hepsetus 1,530
Centropristes striatus 117
Etropus microstomus 91
Merluccius bilinearis 90
Sphaeroides maculatus 59
Pomatomus saltatrix 36
Caranx latus 26
Scophthalmus aquosus 21
Urophycis chuss 15
Pseudopleuronectes americanus 7
Dasyatis sayi 6
Clupea harengus 6
Carcharinus milberti 5
Conger oceanicus 4
Vomer setapinnis 4
Trichiurus lepturus 4
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 21. Species caught by trawling in Chesapeake Bay and the lower York River (Stations 1 to 8), but not taken in other sections of the transect.

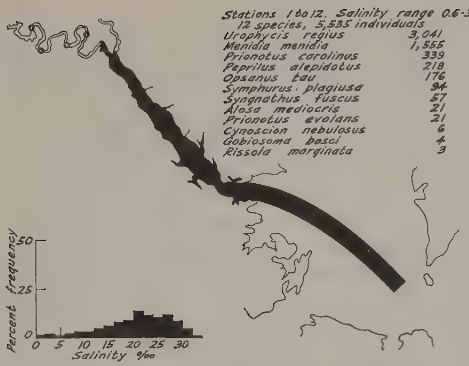
Stations 1 to 12. Salinity range 0.6-32.8‰
12 species, 5,535 individuals
Urophycis regius 3,041
Menidia menidia 1,555
Prionotus carolinus 339
Peprilus alepidotus 218
Opsanus tau 176
Symphurus plagiusa 94
Syngnathus fuscus 57
Alosa mediocris 21
Prionotus evolans 21
Cynoscion nebulosus 6
Gobiosoma bosci 4
Rissola marginata 3
Percent frequency
50
25
0
0 5 10 15 20 25 30
Salinity ‰

Fig. 22. Species caught by trawling in Chesapeake Bay and the York River (Stations 1 to 12), but not taken in the Pamunkey River.

surface in the middle of the stream, as their scarcity in beach-seine hauls in the same area would suggest, they also would be relatively unavailable to a bottom trawl.

The gizzard shad (*Dorosoma cepedianum*) was taken in all sections of the transect, except the lower York River. Obviously, this anadromous species must traverse this section of the river, and its absence from catches in this zone probably merely reflects its relative scarcity in the Chesapeake region, for the total catch was only 36 fish.

The remaining three anadromous fish species, the American shad (*Alosa sapidissima*) and the river herrings (*A. pseudoharengus* and *A. aestivalis*) were taken in all parts of the transect (Stations 1–16) at all seasons. It can be concluded that, although the trawl was not entirely satisfactory for estimating the distribution and relative abundance of anadromous species in the estuary, particularly because it missed the smallest and the largest individuals, it provided valuable information about the seasonal distribution of juveniles. The catches also generally reflected the relative abundance of the various species in the lower part of the Chesapeake.

The catadromous American eel (*Anguilla rostrata*) also was taken at all stations and in all seasons, although not in great numbers. This species is abundant in Chesapeake Bay, as in other Atlantic coast estuaries, but the young are too small and the adults too agile to be caught by trawling in proportion to their abundance.

Seasonal Marine Migrants

The lower part of the estuary (Stations 1–4) yielded the largest number of species of any section or combination of sections of the entire transect (Fig. 20). Twenty-five species were caught exclusively in this zone. All were marine species which spend a part of their lives in the sea, with the possible exceptions of the spotted seahorse (*Hippocampus erectus*) and the striped blenny (*Chasmodes bosquianus*). Neither species is likely to be caught in great numbers in trawls. The seahorses are probably more common in Chesapeake Bay than their occurrence in collections would suggest. They live among marine vegetation close to shore and are not active swimmers. The spotted seahorse, while it occurs near the mouth of the Bay and might occasionally be found outside, is typically a fish of the lower estuary. The striped blenny is common in the Chesapeake region, where it is found frequently on oyster grounds. Although it also could occur outside the Bay, it is not typically a fish of the open sea.

With the exception of scup (*Stenotomus chrysops*), which accounted for 1,513 individual fish of the total catch of 1,637 (more than 90 percent of all fish caught exclusively in this zone), none of these species was taken in great numbers. This was probably because these fishes, including seven species of elasmobranchs, are nearly all active forms which easily could dodge the trawl. Moreover, in the deeper waters of the lower Bay, the trawl was sampling only a small part of the entire water column.

A fairly large number of species (17) was taken in the Bay and the lower York River (Stations 1–8) exclusively (Fig. 21). The striped anchovy (*Anchoa hepsetus*) spawns in the Bay, where its distinctive ovate eggs, together with the similarly shaped eggs of *A. mitchilli,* are common constituents of the summer plankton. This anchovy was not taken in winter, for, as Hildebrand and Schroeder (1928) concluded, it probably leaves the Bay in winter for deeper water. The black seabass (*Centropristes striatus*), which spawns offshore, moves into the Bay when it is about a year old, where it is caught commonly by sport fishermen. Adults of this seabass are not common in the Chesapeake region. The other 15 species are seasonal migrants from the sea.

Twelve species, all marine except the hickory shad, an anadromous species discussed in the previous section, were caught in all parts of the transect (Fig. 22)

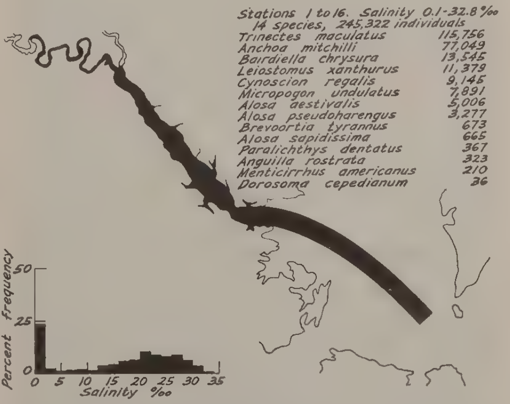
Stations 1 to 16. Salinity 0.1-32.8‰
14 species, 245,322 individuals
Trinectes maculatus 115,756
Anchoa mitchilli 77,049
Bairdiella chrysura 13,545
Leiostomus xanthurus 11,379
Cynoscion regalis 9,145
Micropogon undulatus 7,891
Alosa aestivalis 5,006
Alosa pseudoharengus 3,277
Brevoortia tyrannus 673
Alosa sapidissima 665
Paralichthys dentatus 367
Anguilla rostrata 323
Menticirrhus americanus 210
Dorosoma cepedianum 36
Percent frequency
50
25
0
0 5 10 15 20 25 30 35
Salinity ‰

Fig. 23. Species caught by trawling in all sections of the transect, from Chesapeake Bay to the Pamunkey River (Stations 1 to 16).

from the Bay to the upper York River (Stations 1–12). The spotted hake (*Urophycis regius*), the most frequently caught species in this section, is a winter visitor. It enters the Bay in late fall and winter, reaches its greatest abundance in early spring, and leaves before warm weather arrives. Gunter (1945) described a similar migration pattern in Texas estuaries for a closely related species, *Urophycis floridanus*. The Atlantic silverside (*Menidia menidia*) is one of the most abundant residents of Chesapeake Bay and its tributaries, but its small size and slender body, and its preference for surface waters near shore, make it relatively unavailable to trawls. This silverside enters fresh water (Massmann, 1954), and it is abundant near the entrance of the Bay and probably moves into the sea at times. The oyster toadfish (*Opsanus tau*) is a common inhabitant of the Chesapeake Estuary, where it is considered a pest by sport fishermen. It was taken in the trawl at all seasons, and its sluggish habits and preferred habitat are not consistent with offshore life. The small naked goby (*Gobiosoma bosci*) is a common inhabitant of the shore, not available readily to the trawl, yet it appeared in all sections of the entire transect, except the Pamunkey River. Massmann (1954) took this goby in fresh water in the Pamunkey River. The striped cusk-eel (*Rissola marginata*) commonly remains buried in the bottom and might be passed over by a trawl. Its slender, soft body, also, could easily pass through the meshes of the net.

Marine Fishes Which Use the Estuary as a Nursery Ground

The most interesting group of fishes caught in the trawl were those marine species which were taken in all parts of the estuary, from the mouth of Chesapeake Bay to fresh water in the Pamunkey River (Stations 1–16). Fourteen species exhibited this wide salinity tolerance (Fig. 23), five of which were anadromous or catadromous and have already been discussed. The remaining nine species all were caught in considerable numbers, and the total catch of these nine euryhaline fishes was 236,015 individuals, more than 75 percent of all fish taken in the survey. Obviously, these nine species were important members of the estuarine nekton.

The three species in this group most frequently caught were the hogchoker (*Trinectes maculatus*), the bay anchovy (*Anchoa mitchilli*), and the silver perch (*Bairdiella chrysura*). All spawn in the Chesapeake Estuary, and all are typically fishes of the inshore estuary, although they penetrate fresh water as far as 15 to 40 miles above the upper limit of sea water intrusion (Massmann, 1954), and all enter the sea occasionally. Hence, they are not estuarine animals in the narrow sense. Most of the other species, particularly the spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogon undulatus*), and Atlantic menhaden (*Brevoortia tyrannus*) spawn offshore in late fall or winter, and the young move into the inshore estuaries soon after hatching, often penetrating fresh water in the rivers as much as 25 to 35 miles (Massmann, 1954; Haven, 1957; McHugh *et al.*, 1959; Pacheco, 1962). In fresh or brackish water they spend the winter, growing very little until the water begins to warm in spring. Growth is rapid in spring and early summer, and as they grow, the young slowly move down the tributaries to the Bay. Here the larger individuals join the stocks exploited by commercial and recreational fishermen in fall. Most of these young, now about one year old, leave the Bay with the adults in late fall. Thereafter, they perform an annual migration into the Bay and to the north in spring, offshore and southward in fall.

The weakfish (*Cynoscion regalis*) has a different early life history, spawning in summer, sometimes in the Bay as well as offshore (Massmann *et al.*, 1958). The young spend their first year of life in deep water offshore, then move into the Bay in the spring of the following year. Thereafter, they follow a seasonal migration pattern similar to that described for spot, croaker, and menhaden, offshore and south in fall and winter, inshore and north in summer.

Most species of this group of marine fishes caught in all parts of the trawling survey transect can be found in some part of the inshore estuary in abundance at any time of year. These species are the most abundant fishes in the inshore area and, thus, are the most important members of the estuarine nekton, although in the narrow sense they are not strictly estuarine species. These euryhaline marine species, together with most of the anadromous species and invertebrate nekton like blue crabs and penaeid shrimps, include the estuarine nektonic organisms of greatest value to man. The only important species of this group not of great interest to man at the present time is the hogchoker. Anchovies and menhaden are important as food for commercial and sport fishes. Menhaden, striped bass, and other species of direct commercial and recreational value support some of our most valuable fisheries, not only in sheltered waters, but offshore as well. The greatest biomass of all estuarine nekton, therefore, is composed of fishes which are not confined at all times to the conventionally defined estuary (a river mouth where fresh and salt waters mix). Instead, they enter fresh water, sometimes for important periods of their life, and characteristically, also, leave the river mouth and migrate seasonally to oceanic feeding or spawning grounds. In the sea they may migrate considerable distances without leaving the influence of the river or estuarine environment completely.

It can be no coincidence that the greatest development of anadromous fish stocks has taken place in regions where the offshore estuarine waters are most extensive. Along the Pacific coast of North America, the relatively insignificant inshore estuarine zone, together with the largest offshore estuary in the world, has led to the development of an estuarine nekton community quite different from those along most of our Atlantic and Gulf of Mexico coasts. The estuarine nekton of the eastern North Pacific is dominated strongly by anadromous species. In the western North Atlantic anadromous fishes occupy a secondary position in the estuarine nektonic community, and in the Gulf of Mexico they are virtually absent. The dominant members of most Atlantic estuaries are marine species which perform rather complicated migrations between the inshore and the offshore estuary and, not uncommonly, into fresh water.

Adventitious Visitors

Occasional nektonic visitors to the estuarine environment are not very important members of the nektonic community, but they should not be ignored. No firm dividing line can be drawn between casual and regular seasonal visitors, for some species which are regular seasonal migrants to the inshore estuary may fail to appear when environmental conditions are not favorable, or when their abundance is temporarily reduced. Examples are the bluefish (*Pomatomus saltatrix*), which is notably erratic in its seasonal visit to Atlantic coast estuaries (Hildebrand and Schroeder, 1928), the albacore (*Germo alalunga*) in the Pacific, which failed to appear off the Pacific coast of North America from 1928 to 1934, inclusive (Clemens, 1961), and some of the jacks (*Caranx crysos* and *Selar crumenophthalmus*) along the middle Atlantic coast of the United States (McHugh, 1960). Occasionally, however, pelagic fishes of the high seas stray into Chesapeake Bay, as illustrated by recent records of such species as *Sarda sarda,* the Atlantic bonito (Mansueti, 1962a), *Scomberomorus cavalla,* the king mackerel (Butz and Mansueti, 1962), *Euthynnus alleteratus,* the little tuna (Mansueti and Mansueti, 1962), and the grouper, *Mycteroperca microlepis,* commonly known as the gag (Hoese *et al.,* 1961), and other species (Massmann, 1957). The recent warming of the eastern Pacific Ocean in the period 1957 to 1959 produced many unusual records of southern fishes and sea birds along the North American coast (Radovich, 1960), and some striking changes in distribution and migration routes of salmon and other species (Royal and Tully, 1961; Radovich, 1961). Obviously, meteorological and oceanographic coordinates had shifted considerably with respect to land masses.

Nektonic species other than fishes also appear regularly or occasionally in Chesapeake Bay. Bailey (1946) has cited records of several species of cetaceans, and Schwartz (1962) recorded the occurrence of a little piked whale (*Balaenoptera acutorostrata*) in Maryland waters of Chesapeake Bay. The Atlantic ridley turtle (*Lepidochelys olivacea kempi*) is an occasional visitor (Hardy, 1962).

FISHERIES FOR ESTUARINE NEKTON

Even today, with the rapid development of distant water fishing fleets by several nations, most of the world's marine fish catch still comes from coastal waters. Charts of world distribution of fishing grounds (Walford, 1958; Hela and Laevastu, 1961) show that most fishing is conducted along the continental shelves, and that the most productive marine fishing grounds are close to the continents. In this respect the pattern of world fishing has not changed substantially since 1958. The United States is predominantly a coastal fishing nation, although most of the catch in two of our most valuable fisheries comes from distant waters. Our tuna fleets range thousands of miles from their home ports, taking most of their catch in tropical waters extending below the Equator in the eastern Pacific. Our shrimp fleet in the Gulf of Mexico also ranges widely, taking part of its catch on the Campeche Banks off the Yucatan Peninsula. But these are our only important distant water fisheries. The rest of our catch, over 90 percent of the total United States catch by weight and nearly 90 percent by value, is taken within the limits of our continental shelves, most of it within sight of shore.

Nektonic species make up about 90 percent of the total United States commercial fishery landings by weight and more than 70 percent by value. These are caught principally by three general types of gear: otter trawls and haul seines, which first locate the most productive fishing grounds by trial and error, then concentrate on certain places known to produce good catches; purse seines, which rely mainly upon visual spotting of fish before they can be surrounded; and various forms of fixed or drifting gear, which trap, entangle, or catch fish with baited hooks. Most of these gears work best in shallow water. The techniques of fishing have improved gradually over the years, principally with the advent of power in the form of internal combustion engines. Synthetic twines have permitted construction of larger, stronger, and less bulky nets, and this in turn has allowed mechanical handling methods to be developed to reduce labor costs and speed the operation of gear. Electronic devices for improved navigation, communication, and fish location have brought improvements in efficiency. But, despite all these developments, fishing still is a hunting process, conducted with essentially the same types of gear that were in use 500 years ago.

The world fish harvest is growing steadily. The total catch of 44.72 metric tons in 1962 was almost exactly double the 1951 catch. About 80 percent of this catch consisted of marine nekton, much of which is estuarine-dependent at some life-history stages. The species composition of the United States fish catch probably is typical of world fisheries in general. United States fisheries extend from the arctic to the tropics. At both extremes the major species are estuarine. The Pacific salmons and anadromous trout yielded 315,592,000 pounds worth $56,659,000 to fishermen in 1962. In the same year the shrimp fishery of the South Atlantic and Gulf of Mexico coasts landed 167,804,000 pounds worth $71,832,000, and the menhaden fishery produced 2,347,944,000 pounds with a landed value of $25,866,000. The total catch of these three nektonic estuarine-dependent fishery resources alone was nearly 85 percent of the total weight of fishery products landed by United States fishermen, and nearly 40 percent of the total value (Power, 1964a).

Anadromous Fisheries

Salmons support by far the most important estuarine fishery on the west coast. The great abundance of Pacific salmons undoubtedly is due to a happy combination of circumstances: extensive rivers and lakes that provide adequate spawning and nursery grounds, and a vast and highly productive offshore estuary where large numbers of fish can find sufficient food for survival and growth. It is difficult to escape the conclusion that it is advantageous for anadromous species to remain within the influence of estuarine waters in order to complete their migration. Extensive fishing with gill nets in the North Pacific has shown that salmon remain within the boundaries imposed by vertical and horizontal salinity fronts, with some restrictions imposed by temperature tolerances of the various species (Favorite and Hanavan, 1963; Favorite and Morse, 1964). Nowhere else in the world are there such large stocks of anadromous fishes, or such an extensive offshore estuary.

Extensive stocks of other anadromous or quasi-anadromous fishes support commercial fisheries on the west coast. Foremost among these is the Pacific herring (*Clupea pallasii*), which spawns mostly in the intertidal zone. The young spend most of their first year of life in bays and channels near shore, and there is little evidence that adults migrate far to sea (Kasahara, 1961). The latitudinal range of this herring is so great, however, that some races exist beyond the limits of the North Pacific estuarine zone, utilizing spawning grounds as far south as San Diego Bay. Of some importance also as commercial and recreational species are the smelts (Osmeridae). The eulachon (*Thaleichthys pacificus*) supports commercial fisheries during its spawning migration in major rivers from the Columbia to northern British Columbia. The beach-spawning capelin (*Mallotus catervarius*) and surf smelt (*Hypomesus pretious*) support minor commercial fisheries, but also provide unusual recreational enjoyment reminiscent of the grunion hunts of California beaches (Hart and McHugh, 1944).

Most of the other major fisheries of the Pacific coast exploit demersal species, which cannot be considered truly estuarine. Nevertheless, many of these species have migratory patterns similar to those of typical estuarine forms. The Pacific halibut, for example, moves offshore to the edge of the continental shelf to spawn. Carried by the inshore drift of the bottom waters the young are transported into relatively shallow water. As they grow they slowly shift to deeper, offshore waters (Thompson and Van Cleve, 1936). The fisheries of California, on the contrary, with few exceptions, exploit truly marine species, many of which are pelagic, fast swimming, and wide ranging.

On the Atlantic coast north of Cape Cod, most of the fisheries are for demersal marine species like cod, haddock, redfish, and sea scallops. The less-important estuarine species include Atlantic salmon, river herrings, shad, smelt, striped bass, and a few species of no great commercial value (Stickney, 1959). Atlantic salmon once were much more abundant in most streams, but never as abundant as Pacific salmons. Shad and river herrings are widespread along the Atlantic coast as far south as central Florida. South of Cape Cod the abundance, variety, and importance of estuarine fishes increase. They support extensive commercial and recreational fisheries. The fisheries of Chesapeake Bay afford a typical example which has been discussed already.

Pacific Salmon Fisheries

The salmon fisheries are among the oldest and most valuable fishery resources of the United States. The history of these fisheries in Alaska and the Pacific Northwest States is colorful and romantic, no less so than the story of the Alaskan gold rush. Indeed, the salmon resources are far more valuable than gold, if managed properly, for they are capable of yielding a rich harvest forever. Many of the runs to our Pacific coast salmon streams are not producing maximum yields today. The reasons are complex, but most of the causes would be reversible if the necessary knowledge and the means to put it into effect were available. The subject of salmon conservation is highly controversial, like all fishery problems. There is no doubt that in the rush to make big catches and large profits, many salmon stocks were overfished. Others have been reduced by a variety of causes, including alteration of runoff characteristics and destruction of spawning grounds by careless logging practices; blocks to migration caused by log-jams, hydroelectric power dams, and other obstructions; increased mortality of young by diversion into irrigation canals, injury by turbines, pollution, and temperature and other environmental changes. Serious problems also have arisen from the liberal treaty rights enjoyed by Indians, which allow them to take advantage of fishways and other devices as aids in catching fish. In some parts of the Columbia River system, unrestricted Indian fisheries have nullified expensive salmon conservation measures. Powerful conflicting interests have been involved in the controversy over salmon problems, and many attempts are made to assign the blame for the reduced supply, or simply to look upon salmon as a minor resource of little economic significance. As is common in such matters, events have overtaken the fund of basic knowledge, and controversy has erupted because our knowledge is imperfect. Recently, however, improved federal-state cooperation is making steady progress in resolving mutual problems and gathering the knowledge necessary to develop adequate management procedures. Better knowledge of the spawning escapements necessary to produce maximum yields, and the necessary statutory flexibility to act quickly on current information, have demonstrated that the major Alaskan and Pacific Northwest salmon stocks can be restored to full productivity. Advances in techniques of fish passage over dams, improved hatchery management, installation and successful maintenance of screens in irrigation diversions, and other accomplishments in the Columbia River system are showing how this important salmon river, rapidly being converted into a chain of lakes, can contribute its full share to the nation's fishery harvest.

The timing of salmon runs to the various tributaries of the home stream is so precisely balanced that there can be little doubt that each spawning ground has its own genetic race (Thompson, 1959). This is evident especially in large streams with many spawning areas, some remote, some near the sea. The timing of runs, and the energy reserves of the individual stocks, are nicely adjusted to carry them to their destination. To obtain maximum sustainable yields from such resources, it is necessary to fish each race selectively. It is impossible to achieve perfection in terms of maximum weight harvested, for in order to do this it might be necessary to harvest each genetic unit on or near the spawning ground. The physiological changes that take place during the struggle to reach the spawning grounds quickly reduce the quality of salmon as human food. The great cost of harvesting many small population units at widespread and inaccessible locations would make such a management scheme impossible economically. Accordingly, it is an accepted policy in the United States and Canada to confine salmon fishing to restricted zones near the mouths of the streams, relying on knowledge of timing of runs to various spawning areas to allow adequate escapement. In this way, American salmon fisheries achieve the maximum yield consistent with maximum quality of fish. Thus, the valuable salmon fisheries of the Pacific coast of North America are truly estuarine fisheries, even in the narrow sense, for they are conducted in estuarine waters.

Although the United States and Canada prevent the nationals of their own countries from fishing for salmon on the high seas, these domestic laws do not apply to citizens of other nations on the high seas beyond our territorial limits. There is considerable disagreement among nations as to whether the doctrine of freedom of the seas can be interpreted as including freedom to fish everywhere in international waters. Many important estuarine nektonic resources, for example, move freely from territorial to international waters and back again. The Japanese high seas fishery for salmon in the North Pacific Ocean provides an excellent example of the problems that arise under such circumstances (Konda, 1963; Allen, 1964; Johansen, 1964). After the end of World War II, Japan resumed her high seas fishery for salmon in the North Pacific. Exploratory expeditions to the eastward to test high seas salmon potential had been terminated in the 1930's under strong pressures from the United States. In order to minimize the effects of this high seas fishery upon American stocks of salmon the United States and Canada concluded a treaty with Japan in 1953 under the terms of which Japan agreed to abstain from fishing salmon east of 175° W. longitude. When the treaty was negotiated very little was known about the distribution of salmon on the high seas. It was assumed that significant numbers of salmon of North American origin did not migrate westward of this line, which approximately bisects the North Pacific Ocean. Subsequent research, which was marked by development of a number of ingenious new techniques, has shown that these basic assumptions were not valid. Not only do large numbers of red salmon from the valuable Bristol Bay stocks migrate far to the west of this line, but also large numbers of pink and chum salmon of Asian origin move far to the east (International North Pacific Fisheries Commission, 1964). Japanese fishermen have an opportunity to harvest these Asian salmon as they move westward again on their spawning migrations. They are not vulnerable to fishing by Canadian and United States fishermen, who are restricted by law from fishing for salmon with nets on the high seas. But there are no similar restrictions upon Japanese fishermen west of the line, and they take substantial numbers of Bristol Bay red salmon and some other salmon species each year prior to the spawning migration. This indiscriminate fishery cannot be controlled with respect to its catch of individual stocks, and it could well exceed the allowable surplus of some stocks before the American fishery has an opportunity to begin its harvest. Moreover, the Japanese fishery takes large numbers of immature fish. The argument that indiscriminate high seas salmon fishing would overexploit some stocks and underexploit others, thus leading to smaller sustainable yields than a controlled inshore fishery, is a compelling one. Recent evidence that growth exceeds losses by natural mortality even during the ocean phase of the spawning migration has removed all reasonable doubt that high seas fishing is wasteful of the salmon resource (Ricker, 1962; R. A. Fredin, personal communication). The principle of abstention, upon which the present treaty is based, holds that if a nation is taking the entire surplus yield of a resource, and is conducting extensive scientific research upon which is based an effective management program designed to obtain the maximum sustainable yield, no other nation should enter the fishery for that resource. This principle is particularly applicable to the salmon resources, for unrestricted entry of other nations into these fisheries could lead very quickly to a breakdown of American management measures. If this should occur, uncontrolled fishing by our own fishermen could destroy the major American salmon stocks, leaving nothing for anyone to take.

Atlantic Shrimp and Menhaden Fisheries

Although they are quite different biologically, the shrimp and menhaden of the Atlantic and Gulf of Mexico coasts of the United States are so similar in respect to the basic features of their life histories that they can be considered together. Several species of each are involved, but the essential details are the same. Both groups spawn in the ocean. The newly hatched young find their way very quickly into coastal waters, penetrating far into the estuaries and salt marshes. Postlarval menhaden often are found in waters of very low salinity (Gunter, 1956; Massmann, 1954). Tiny shrimp infiltrate the shallow waters of the protected coastal marshes. These delicate early stages thus overwinter in a rigorous environment, subject to sudden and large changes in temperature, salinity, and other physical factors. There is some evidence that these environmental changes on the nursery grounds account for the large fluctuations in abundance characteristics of these species. In addition, these valuable resources often undergo their early development in waters that are particularly vulnerable to the effects of man's activities. Our rapidly increasing human population and industrial development have brought about great changes in the inshore environment, many of which could be adverse for estuarine species. There is great concern at present that these developments will outpace our scientific knowledge, and that the resources of the estuaries may be doomed.

Other Commercial Estuarine Fisheries for Nekton

Although the Pacific salmons and Atlantic menhadens and shrimps are our most important estuarine nektonic resources of commercial value, they are by no means the only such species. On the Pacific and Atlantic coasts of the United States and Canada the anadromous shad, striped bass, and smelts support commercial fisheries of considerable local importance whenever they occur in abundance. In the Atlantic the anadromous river herrings also are important. As already described, truly inshore estuarine environments are not extensively developed along the Pacific coast of North America. The Pacific herring, which shows some affinity for waters of reduced salinity (Kasahara, 1961), and a few species like the starry flounder (Alverson *et al.*, 1964), which prefer the inshore environment at certain life history stages, also can be classed as estuarine nekton. But a substantial part of the nektonic community of the waters over the continental shelf along our west coast is composed of marine species with no apparent estuarine requirements.

Along the Atlantic and Gulf coasts of North America, on the other hand, most of the nektonic animals enter the inshore estuaries at times, and many spend important parts of their lives in waters of reduced salinity, as has been described already. Croakers and weakfishes, anchovies and herrings, butterfishes, flatfishes, jacks, and mullets are characteristic and abundant fishes of Atlantic and Gulf of Mexico inshore estuaries.

No special biological significance needs to be attached to the rather great differences in estuarine nektonic fauna of the Atlantic and Pacific coasts of North America. The dominance of anadromous species and relatively minor importance of coastal estuarine species can be attributed largely to the rugged coastal topography, relatively heavy runoff, and great tidal mixing in the north; the narrow continental shelf, arid climate, and coastal upwelling of high-salinity water off southern California; and the general pattern of oceanic circulation in the whole North Pacific. It is interesting that several of the major estuarine nektonic species of Pacific Northwest waters also enter oceanic waters off central and southern California, and several typically marine fish species of the California and Baja California coast commonly enter estuarine waters farther north. The king salmon (*Oncorhynchus tshawytacha*) and steelhead trout (*Salmo gairdneri*) range as far south as the Sacramento River and must traverse oceanic waters beyond the limits of the offshore estuary as they migrate back and forth to their native streams. The Pacific herring (*Clupea pallasii*), which favors low-salinity waters in the northern part of its range, also is found in oceanic waters in the vicinity of San Diego. The Pacific sardine (*Sardinops caerulea*) and Pacific northern anchovy (*Engraulis mordax*), which are strictly marine species in the major parts of their ranges, also enter estuarine waters along the British Columbia coast (Clemens and Wilby, 1961).

The dominance of fishes often called estuarine-dependent forms, and the secondary importance of anadromous species, along the Atlantic and Gulf coasts also can be attributed to topography and oceanic circulation. The generally low-lying coast, with its great development of shallow sounds and semi-enclosed drowned river valleys and coastal lagoons with extensive salt marshes, provides protected and highly productive nursery and feeding grounds. The Gulf Stream interposes an abrupt salinity and temperature barrier along the general line of the edge of the continental shelf, close to the coast from Florida to Cape Hatteras and in a widening band from Hatteras to the Grand Banks (Bigelow and Sears, 1935; Fuglister, 1963). This probably accounts for the rather sharp distinction between oceanic and estuarine nekton in the Atlantic, as compared with the virtual absence of an inshore estuarine nektonic fauna along the Pacific coast, where the salinity and temperature gradients are more gradual.

Estuarine Sport Fisheries

The recreational fisheries are not commonly thought of as commercial fisheries, although a considerable group of industries has developed in the United States to provide sport fishermen with bait and other supplies and materials and to provide services for enjoyment of the sport. Moreover, an unknown proportion of the sport catch of Pacific salmon, Atlantic bluefish, and other valuable food fishes enters commercial markets. Of greater interest to scientists studying commercial fishery resources, however, are certain other aspects of sport fishing which influence the commercial fisheries. The growing sport fisheries are already taking substantial numbers of certain species of commercial value, such as coho and chinook salmon in the Pacific (Kasahara, 1963) and a variety of species in the Atlantic, including shad, striped bass, scup, flounder, croakers, and weakfish (Younger and Zamos, 1955; Shearer *et al.,* 1962; Richards, 1962; Belden Associates, 1961; Harmic, 1956). This development raises two interrelated problems for the commercial fisheries. It means that sportsmen are taking a growing share of the annual harvest, a share which for some species already equals or exceeds the commercial catch. It means that an increasingly large part of the total catch is being taken by a diverse fishery for which no adequate biological statistics are now available. These problems are of growing concern to fishery scientists, who, as yet, can see no practical method for obtaining detailed information necessary for wise management of these joint fisheries.

The proliferation of saltwater sport fisheries, which predominantly exploit stocks of estuarine nekton, has brought about growing pressures of a social-political nature on the commercial fishing industry. These concern the effects, or supposed effects, of commercial fishing operations on sportfish resources. The two most efficient types of commercial fishing gear, purse seines and otter trawls, have come under the greatest public criticism, without a shred of solid scientific evidence to support the contention that these gears deplete the food supply of sport fishes, or that they kill large numbers of sport fishes.

The purse-seine fisheries for herring, sardines, and anchovies on the west coast, and for menhaden on the Atlantic and Gulf of Mexico coasts, have been under criticism on these grounds for many years. The opposition has been so effective in California that it is prohibited to land sardines and anchovies in that state for direct reduction to meal and oil. Fishery scientists believe that this legal barrier has led to substantial underutilization of the Pacific anchovy resource. In Alaska determined opposition to herring fishing for reduction has been led by a segment of the commercial fishing industry, the salmon trollers, who believe that herring are a major food of chinook and silver salmon.

Opposition to menhaden purse-seining has been growing more intense along the Atlantic and Gulf coasts as recreational use of the beaches and estuarine waters increases. Each year bills to prohibit menhaden fishing in estuaries receive serious consideration in one or more state legislatures. The scientific evidence leads to the conclusion that such measures are unnecessary and would lead to economic waste of a valuable resource. Public opinion, however, will continue to draw conclusions adverse to the menhaden industry as long as the fishery continues to operate within sight of large numbers of uninformed people, especially if fishing boat captains sometimes appear to exhibit a lack of consideration for the recreational users of the estuaries. A detailed account of the problem as it affects the Gulf of Mexico fishery has been published recently by Gunter (1964). An additional argument in favor of menhaden fishing, not discussed by Gunter, is that menhaden may consume large quantities of larvae of other valuable estuarine nektonic species (McHugh, 1962). This raises interesting questions about the relationships between abundance of menhaden, shrimps, blue crabs, and other resources, which merit scientific attention.

The activities of trawlers, especially those that fish shrimps in enclosed estuarine waters, also have been questioned by sport fishermen and others. Trawls capture large numbers of unmarketable fishes, many of which are the young of species of recreational and commercial value. Scientists have generally agreed that this "destruction" is not serious, and shrimp trawling has not been prohibited by any coastal state for this reason. Otter trawling is prohibited in Chesapeake Bay by Maryland and Virginia, and elsewhere in territorial waters by other states because its efficiency is considered inconsistent with conservation. Much more research needs to be done on the alleged destructiveness of trawls.

Many scientists find the social-political aspects of fishery science distasteful. Many academic scientists are critical of their colleagues in fishery science who must conduct their scientific research, and must attempt to apply the results effectively, in what appears to be a completely non-scientific and unsympathetic atmosphere. The inconsistencies that seem to characterize much of the work of the fishery scientist tend to become less acute when it is considered that fishery science is a branch of ecology which extends its attention to man's activities and attitudes as an important set of environmental phenomena that influence the biology and dynamics of fishery resources (McHugh, 1962).

MAN AND ESTUARINE NEKTON

Man has been cited already as an important member of the nektonic community of estuaries. His growing activities as a modifier of the environment are the subject of another paper in this volume and need not be repeated here. His role as a predator, catching marine animals for recreation or for profit, has been substantial for centuries. This source of mortality is increasing rapidly as man increases in numbers. According to the best estimates available (F.A.O., U.N., 1963) the world harvest of fishery products has about doubled since 1951. Some scientists have argued that with present fishing gear and methods, the sustainable harvest of protein from the sea might be increased five- to tenfold. This is largely speculation, however. Other fishery scientists have been much more pessimistic (Graham and Edwards, 1962; Meseck, 1962).

Few nations are dedicated to the principle of fishery conservation for maximum sustainable yields in the sense understood by the United States, Canada, and certain Western European countries. In the rush to increase the world supply of protein food, several countries have expanded their high seas fisheries to a remarkable degree in the last 15 years or so. Foremost among these countries are Japan, the U.S.S.R., Peru, and Communist China. The United States, once second only to Japan as a fish producer, now has dropped to fifth place. Our total annual fish production, including industrial fish, increased very rapidly in the 1920's and early 1930's, but in the last 30 years has grown at a rate of less than one percent per year. Our steady annual per capita consumption of about 10.5 pounds has not stimulated domestic food-fish production, which has remained approximately constant for about 30 years. The extra supply needed to maintain a constant rate of consumption by a growing population has been met by a steady rise in imports. In 1963, for the first time in history, the United States imported a greater weight of edible fishery products than her own fishermen produced (Power, 1964b). Faced by higher standards of living and higher costs for labor, materials, and equipment than foreign competitors, American fishermen have failed to maintain and modernize their equipment. The gap in efficiency and cost of production between domestic and foreign fishermen is widening steadily in most segments of our fishing industry.

Foreign fleets of highly efficient mother ships and catcher boats are operating close to our shores in many regions. There is no reason to expect that this activity will decrease. With some exceptions these foreign fleets are not seeking species traditionally harvested by our own fishermen. But incidental catches of certain species valuable to us are inevitable. Such catches, if they are at all substantial, will reduce the surplus available to our own fishermen, and will greatly complicate our management programs. We have not been aggressive in developing distant water fisheries to compete on an equal basis in the world ocean with our foreign competition. Our only successful distant water fisheries are for high priced species, such as tuna and shrimp, uniquely attractive to the American consumer. Although foreign fleets fishing off our coasts are seeking, primarily, species not being utilized fully by American fishermen, this is not entirely so. Japan is competing with our fishermen for salmon, halibut, tuna, crabs, and other valuable species. The U.S.S.R. is fishing crabs in the Gulf of Alaska and groundfish off New England, and is extending her operations to all sections of our coast including the Gulf of Mexico, showing an interest in such important United States estuarine resources as menhaden (*Brevoortia* spp.) and herring (*Clupea harengus*). The threat to traditional American fishery resources grows steadily.

The fishing industry of the United States also faces serious domestic problems. High costs are a major cause of these difficulties, but these costs could be reduced in many ways by appropriate legislative action. With few exceptions, fishery laws and regulations in the United States are subject to local legislative controls. Thus, local traditions and beliefs and special interests exert a strong influence upon fishing operations. It is common in the United States, as in many other parts of the world, to believe that increased efficiency is contrary to the principles of conservation. Consequently, many kinds of fishing gear or methods are prohibited or severely restricted. Many examples of such restrictions could be cited, but a few will suffice to illustrate how fishing is regulated by enforced inefficiency. The problem is complicated by the fact that fishery resources in the territorial waters of the United States are under the control of the individual states. The philosophy of fishery management varies widely from state to state, and fishery laws and their enforcement consequently differ from place to place. In Alaska fish traps are illegal and salmon purse-seine vessels cannot exceed a certain size. In California it is illegal to fish anchovies for manufacture of fish meal or oil. In Virginia it is illegal to use any gear other than hand-operated tongs to remove oysters from most naturally-producing grounds. In Maryland, purse seines are illegal. In Massachusetts and some other states control is exerted at even lower political levels, for shellfish regulations are made and enforced by the county or the town.

These restrictions have nothing to do with conservation per se. They are popular because traps are highly efficient for catching salmon in certain locations and the privilege of using certain sites confers exclusive property rights. It is recognized that large fishing vessels can operate large nets which catch greater quantities of fish. It is contended that the use of anchovies and other fishes for fish meal manufacture is wasteful, because such small fishes are important food for larger carnivorous species, many of which are important to sport fishermen. It is believed that mechanical harvesting of oysters on naturally producing grounds would overharvest the resource and damage the bottom for setting of future crops. It is thought by many that the capture of menhaden and other schooling fishes by purse seines not only depletes the food supply of other important commercial and game fishes, but also catches large numbers of the more valuable species. Much of the opposition to more efficient types of gear stems from a prevailing belief that increased efficiency is synonymous with destruction. It is difficult to reconcile the conservative attitude toward increased catching efficiency with the progressive American attitude toward technological development which characterizes almost all other United States industries today, including agriculture. Perhaps this apparent anomaly is not as contradictory as it seems, however, for although there is nothing in the desire for greater efficiency that is inconsistent with the need for conservation of the resource, each improvement in the fish catching operation implies stricter control on total effort and total catch. There is a deeply rooted tradition that the resources of the sea are common property. This tradition carries with it a resistance to legislative interference with this right. Statutory restrictions on efficiency of harvesting tend to distribute the catch among a greater number of fishermen and place economic limits on the total catch which have somewhat the same effect as conservation measures. The inevitable result, however, is an economically weak fishing industry. With a few notable exceptions the domestic fishing industry of the United States is in this unenviable position today. Resistance to technological improvements in the fish catching operation might be alleviated if practical techniques to increase the yield of the sea were available, for then the fear of overfishing could be balanced to some extent by increased productivity. In a democracy like the United States, however, the only final way to achieve efficient increases in marine productivity would be under a system of private enterprise. Common property resources like the living nektonic resources of estuarine waters are not easily amenable to private management. It will be difficult enough to obtain the social and legal concessions necessary to bring the more tractable molluscan shellfish resources under a progressive system of private enterprise.

Author's Note: The manuscript was written about two years ago. In the interim new developments have altered the condition of certain stocks of estuarine nekton or have led to social and political changes which affect the accuracy of certain statements. The concluding sections of this paper are affected particularly, and it is appropriate to append these comments to bring these sections, "Fisheries for Estuarine Nekton" and "Man and Estuarine Nekton", up to date.

World fish catch—The world fish catch continues to increase. In 1966 it may approach 60 million tons, a 25 percent increase over the figure cited for 1962. Recent information suggests that the large fish production of mainland China is mainly from fresh waters and that she does not rank among the leading producers of marine fishery products.

Marine sport fish catch—Marine sport fisheries are growing in importance in the United States, and a very large part of the ocean catch is made in estuaries. Although detailed statistics are not available, conservative estimates place the present annual United States marine sport fish catch at about 11 percent of the weight of the total commercial catch, or about 267,600 metric tons (McHugh, 1966). Recreational and subsistence catches of estuarine nekton throughout the world probably represent an important unrecorded segment of the total world catch.

California anchovy fishery—Recent studies in California (Murphy, 1966) have provided convincing evidence that the total biomass of California sardine and anchovy (*Sardinops caerulea* and *Engraulis mordax*) has remained relatively constant as the sardine has declined in abundance. Armed with this evidence, scientists and others have been able to convince appropriate authorities that a controlled anchovy fishery for reduction to oil and meal will provide valuable ecological information with no danger of damage to the resource. Limited fisheries for anchovy have been allowed in 1965 and 1966, and the results will be awaited with interest.

Consumption of fish and fishery products in the United States—It has been said repeatedly that the annual per capita consumption of commercially caught fish and shellfish in the United States has remained steady for many years, at an average between 10 and 11 pounds. It has not always been made clear that this refers only to edible fishery products used directly as human food. Domestic production and imports of fishery products for other purposes, especially fish meal and scrap, have been increasing steadily. Much of this is used as a supplement in the diet of poultry and other livestock and thus is converted into human food. If all fishery products consumed in the United States are included, annual per capita consumption has been increasing for some time. From 1946 to 1964, for example, total consumption rose from 5.3 to 12.0 billion pounds. Average per capita consumption has increased from 39.4 pounds in the five-year period 1946–1950 to 57.7 pounds in the period 1961–1965.

An unknown, but probably increasing, commercial harvest of freshwater fishes, especially trout, carp, and catfish, is being produced in the United States. This production is not included in fishery statistics published by the Federal Government. Fish farming apparently has been much more successful in our fresh waters than it has in estuaries.

Improvement of fishing methods in the United States—In comparing efficiency and costs of production of domestic and foreign fishermen, a clear distinction must be made between high seas operations and local fisheries in territorial waters. Our distant water tuna fleet is a model of efficiency which more than holds its own against foreign tuna fleets. Even the struggling New England groundfish industry has found that it can compete successfully with large foreign factory ship fleets if it is provided with modern vessels and gear. Within coastal waters, however, along many sections of our coast, the cost of catching fish and shellfish is unnecessarily high because local laws and regulations often limit efficient operation. It is clear that the United States fishing industry can operate competitively with foreign fishermen if it can obtain the necessary capital and can surmount institutional barriers.

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Randomness in Distribution of Pink Salmon Redds

Pink salmon (*Oncorhynchus gorbuscha*) deposit their eggs in beds of spawning streams about 8 months before the fry emerge and migrate to sea. Less than 25% of the eggs deposited by the parent spawners survive the period of freshwater residence (including upper intertidal areas of streams, where pink salmon commonly spawn).

Competition for space on spawning grounds may cause mortality of the spawn of salmonid fishes (Gilbert and Rich, 1927; Hobbs, 1940; Alm, 1950; Krogius, 1951; Allen, 1951; Morgan and Henry, 1959), and mortality from superimposition of redds increases as the density of spawners increases (Smirnov, 1947; Kaganovskii, 1949; Semko, 1954; Horton, 1961; McNeil, 1964).

Three general hypotheses about the distribution of redds within a spawning area are possible: (1) hypothesis of uniform dispersion — once a redd has been dug, there is decreased likelihood of further digging at the same location; (2) hypothesis of random dispersion — redds are dug at random locations; and (3) hypothesis of contagious dispersion — once a redd has been dug, there is increased likelihood of redigging at this location.

In an earlier paper (McNeil, 1964), I described observations on the success of spawning pink salmon and developed a mathematical model to describe egg recruitment to a spawning bed. The model was based on the hypothesis of random dispersion of redds and was used to predict mortality of eggs from superimposition of redds with different densities of spawners.

This hypothesis was tested by evaluating the occurrence of digging by pink salmon at particular locations within a spawning area of Lovers Cove Creek near Little Port Walter on Baranof Island, southeastern Alaska, in September and October 1965. Experimental methods and results are described in this report, and questions of overestimation and underestimation of mortality from a model based on an assumed random dispersion of redds are discussed briefly.

Methods.— The study area (Fig. 1) was 202 m² (3.05 m × 66.14 m) and was one part of an artificially constructed spawning channel having an area of 223 m² (3.05 m × 73.15 m). The gradient was a uniform 0.75%, and pools were located immediately downstream and upstream from the area. The composition of bed materials showed no obvious variations from the head of the channel to the bottom. Unspawned adult pink salmon for the study were captured in four traps as they entered the stream to spawn and were released in the study channel.

The occurrence of digging by pink salmon spawners at a particular location was indexed through the release of a buoyant table tennis ball buried 8 cm in the spawning bed. Each ball, 3.8 cm diam, was numbered to identify the location of its point of burial. Balls were placed at 216 locations in columns and rows (Fig. 2).

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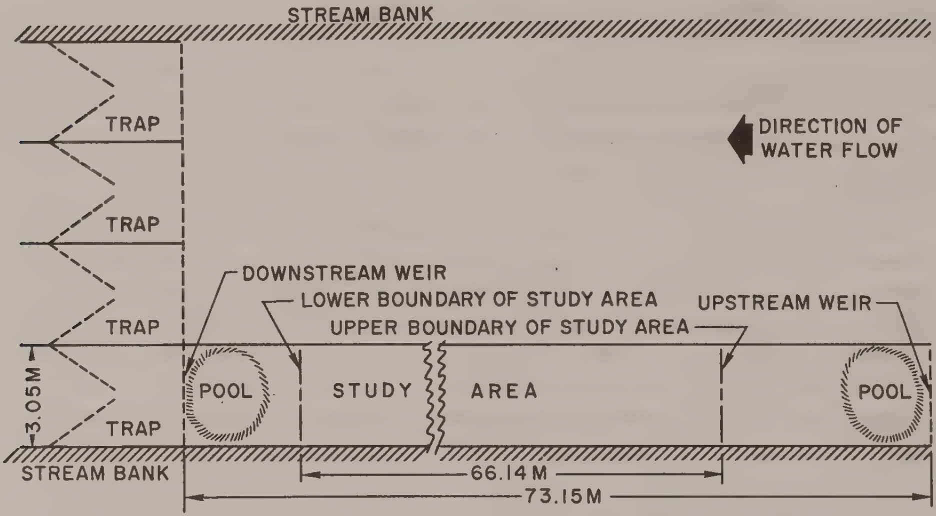
STREAM BANK
TRAP
TRAP
TRAP
TRAP
DIRECTION OF WATER FLOW
DOWNSTREAM WEIR
LOWER BOUNDARY OF STUDY AREA
UPPER BOUNDARY OF STUDY AREA
UPSTREAM WEIR
3.05 M
POOL
STUDY AREA
POOL
STREAM BANK
66.14 M
73.15 M

FIG. 1. Study channel in Lovers Cove Creek, southeastern Alaska, showing locations of traps, pools, and study area.

A preliminary study on the configuration of pink salmon redds indicated that balls buried 8 cm deep would be released by pink salmon spawners digging redds. In that study, the configuration of six redds was evaluated from release of table tennis balls buried at 217 locations within a 20.2 m² study area. The balls were stacked one upon another in columns consisting of seven balls each. The shallowest ball was buried 4 cm and the deepest 27 cm. The columns were spaced at intervals of 0.3 m. Each ball was marked distinctively to identify its location and depth of burial. The average area of the six redds determined from the released balls was 1.1 m², and the average depth was 9 cm. The maximum depth ranged from 11 to 19 cm.

Unspawned pink salmon placed in the experimental section of the Lovers Cove Creek channel numbered 195 females and 228 males — an average density of 0.87 female per meter². The fish spawned from September 11 to

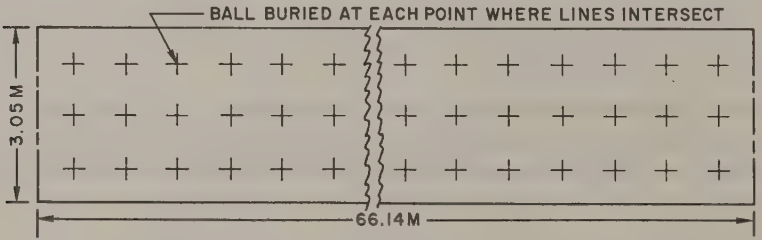
BALL BURIED AT EACH POINT WHERE LINES INTERSECT
3.05 M
66.14 M

FIG. 2. Arrangement of table tennis balls in creek. Distance between balls was approximately 0.9 m and distance between outside balls and nearest boundary of the study area was approximately 0.6 m.

October 6. Balls released from the streambed by spawners that were digging redds floated and were retained by the downstream weir (Fig. 1).

Once a day the balls were collected, recorded, and reburied at their former locations. The first balls were collected and reburied September 11 and the last October 5. The experiment continued 25 days.

The number of times a location containing a ball had been dug by spawners was indexed by the number of times the ball had been released from the streambed. One release of a ball within a 24-hr period was counted as one occurrence of digging at a particular location. To obtain information on randomness in the distribution of redds, the observed numbers of locations from which balls had been released 0, 1, 2,. . . times were compared with the expected numbers calculated from the Poisson and negative binomial probability distributions.

Results.— Balls were released from the spawning bed 157 times. Individual balls were released 0 to 5 times (average, 0.73). The observed occurrence of releases and the expected occurrences from the Poisson and negative binomial distributions are given in Table I.

TABLE I. Observed occurrences of balls released from Lovers Cove Creek study area 0, 1, 2, 3, 4, 5, and >5 times and the expected occurrences from the Poisson and negative binominal probability distributions with the same mean. (The mean number of releases per location is 0.73; the variance is 0.934.)

No. of releases	Observed occurrence	Expected occurrence from Poisson distribution	Expected occurrence from negative binominal distribution[a]
0	116	104.4	113.2
1	59	75.9	64.8
2	29	27.6	25.6
3	10	6.7	8.7
4	0	1.2	2.7
5	2	0.2	0.8
>5	0	0.0	0.3
Total	216	216.0	216.1

[a] Expected values were from probabilities of the negative binominal distribution for $\bar{x} = 0.73$, $\hat{k} = 2.6$, and $s^2 = 0.94$ given by Williamson and Bretherton (1963.)

One property of the Poisson distribution is that mean and variance are equal, and it is convenient to test the observational data for equality of mean and variance with chi-square. By this test, the sum of the squared deviations of the individual observations (x_i) from the sample mean ($\bar{x}$) is divided by the sample mean:

$$\chi^2\,(n{-}1\text{ df}) = \frac{\sum_{i=1}^{n} (x_i-\bar{x})^2}{\bar{x}} \qquad \ldots\ldots(1)$$

A χ^2 value of 275 (df = 215; $P \simeq 0.004$) was obtained, and the hypothesis that mean and variance are equal was rejected. The variance was significantly larger than the mean.

A goodness-of-fit test applied to data on the Poisson distribution yielded a χ^2 value of 7.00 (df = 3; $P \simeq 0.08$). For this test, four or more occurrences of balls released from the study area were combined to avoid expected values less than 1.0.

When variance is greater than the mean, the negative binomial distribution sometimes describes events better than the Poisson. The negative binomial is a unimodal distribution and applies where occurrence of an event (i.e. release of a ball from a particular location) is associated with increased probability of recurrence of the event. It is defined by the population mean (μ) and a coefficient (k), the value of which depends upon the degree of contagion; and it converges to the Poisson as contagion disappears.

The coefficient of dispersion (k) can be estimated from the sample mean and variance (s^2) by

$$\hat{k} = \frac{\bar{x}^2}{s^2 - \bar{x}} \qquad \ldots\ldots(2)$$

(Williamson and Bretherton, 1963). In the present study, $\hat{k} = 2.6$. The relative efficiency of this estimator, which is derived by the method of moments, as compared with a maximum-likelihood estimator is at least 90% (Williamson and Bretherton, 1963).

A goodness-of-fit test applied to data on the negative binomial distribution (Table I) gave a χ^2 value of 2.09 (df = 2; $P \simeq 0.40$). Again four or more occurrences of balls released from the study area were combined to avoid expected values less than 1.0. The observed occurrence of release of balls is in good agreement with the expected occurrence and shows improvement over the Poisson distribution.

Discussion and Conclusions.— Because a female pink salmon spawner occupies a territory and defends it against intrusions by other females, the hypothesis of uniform dispersion in the distribution of redds is attractive. There are, however, at least three possible contradictions to the hypothesis of uniform dispersion: (1) pink salmon may spawn in darkness when territorial defense by female spawners may be ineffective; (2) females may retain the capability to protect their redds for only a short period, even though they may remain on the spawning ground over a long period; (3) certain locations may be sufficiently attractive to spawners for them to overcome females defending territories.

The hypothesis of random dispersion of redds is also attractive because it provides for the development of a relatively simple model of spawning success (McNeil, 1964). If dispersion of redds were uniform, the model of random dispersion would overestimate mortality from superimposition. If dispersion were contagious, the model of random dispersion would underestimate mortality from superimposition. The pattern of release of balls from the Lovers Cove Creek study supports the hypothesis that dispersion of redds is contagious.

The importance of contagious dispersion of redds as a source of error in a model of egg recruitment to a spawning bed based on an assumed random dispersion depends on the relative values of k and μ. The population variance (σ^2) and mean are related empirically in the negative binomial distribution by

$$\sigma^2 = \mu + \frac{\mu^2}{k} \quad \ldots\ldots(3)$$

Thus, as μ becomes small or k becomes large, $\frac{\mu^2}{k} \to 0$, and

$$\sigma^2 \to \mu \quad \ldots\ldots(4)$$

Equation 4 approximates the relationship between the mean and variance of the Poisson distribution; thus contagious dispersion of redds could be relatively unimportant where k is relatively large in comparison with μ. Where k is small in comparison with μ, a model of egg recruitment based on random dispersion of redds would underestimate mortality from superimposition of redds.

Additional study might establish if contagious dispersion in the distribution of pink salmon redds is general in natural situations and if contagion is considerable or slight. Because the degree of contagion may relate to uniformity of habitat and density of spawners, these variables should receive consideration. In the Lovers Cove Creek channel, the gradient of the bed was uniform, and size composition of bed materials did not vary in any obvious manner from the head of the channel to the bottom. At the average density of 0.83 female per meter^2, I estimated $k = 2.6$ and $\mu = 0.73$. Here the relatively large value of k in comparison with μ suggests that contagion was slight. The model of egg recruitment based on random dispersion of redds would not in this circumstance lend to a serious underestimate of mortality from redd superimposition.

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With the British to Antarctica

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(All photos by author)

The United Kingdom has long been active in Antarctica, beginning with Cook's first crossing of the Antarctic Circle in 1773 and continuing through two centuries of exploration by such men as Weddell, Biscoe, Ross, Scott, Shackleton, and the present Director of the British Antarctic Survey, Sir Vivian Fuchs. Feats of exploration of the "White Continent" by this succession of British heroes have fired the enthusiasm and admiration of their countrymen and have resulted in sustained public support of British expeditions. Since 1943, the British have been continuously active in the region. From 1946 to 1961, scientific and exploratory activities were conducted by the Falkland Islands Dependencies Survey and since then by its successor, the British Antarctic Survey (BAS).

In the 1966-1967 season, exchange representatives from France and the United States accompanied the British resupply expedition. They were M. Pierre Rolland, Governor of French Southern and Antarctic Territories, and I, a fishery research biologist. Sir Vivian Fuchs, famed for his transantarctic traverse in 1957-1958 (during the IGY), accompanied the resupply expedition for the first time in several years. His thorough inspection of all British activities and facilities presented a unique opportunity to the foreign representatives to become acquainted with all aspects of the British operation. Our route and the locations of the bases visited are shown in Fig. 1.

Early in 1967, the support of scientific agencies by the British government underwent a reorganization which affected BAS. Formerly, BAS was under the Colonial Office, with the Governor of the Falkland Islands serving as its political head. The Governor is also High Commissioner of British Antarctic Territory. Now, BAS is under the National Environmental Research Council (NERC). The actual leadership of BAS remains centered in its Director, Sir Vivian Fuchs.

The British method of operation in Antarctica differs from that of the United States in two fundamental ways: It depends little on military services for logistic support, and its leadership is strongly centralized at each base through a director-commander who has absolute authority in all matters. The system has worked well over many years.

The British have no long-range aircraft in Antarctica and, therefore, depend entirely on ships for the transport of supplies and personnel to and from the Continent. Two Royal Research Ships, *John*

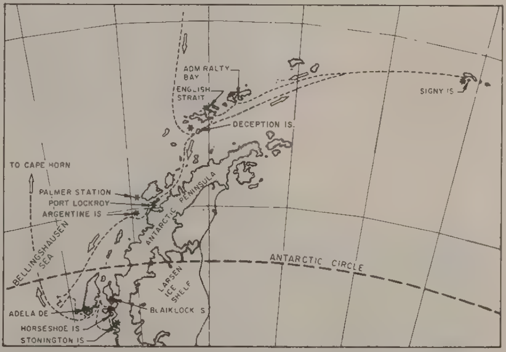

Figure 1. Author's travel route and location of British Antarctic Survey bases.

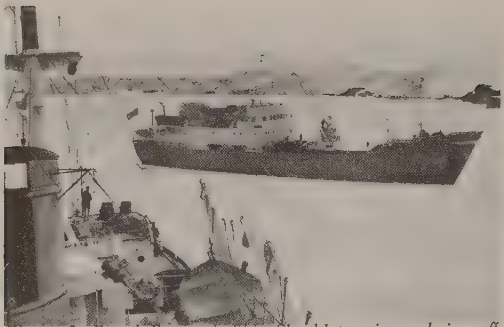

Figure 2. Royal Research Ship Shackleton *in pack ice off Adelaide Island Base. RRS* John Biscoe *in foreground and, in the distance, Fuchs Ice Piedmont, which British light planes use as a landing field.*

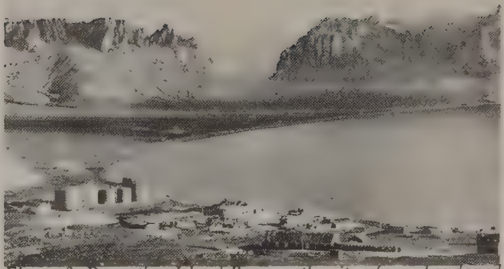

Figure 3. Deception Island Base on the site of an abandoned whaling station in drowned volcanic crater. New British fiber glass hut is in lower center.

Biscoe and *Shackleton* (Fig. 2), constitute the backbone of BAS logistics. Each summer from October to March, the 200+-foot, ice-strengthened cargo and personnel carriers service and resupply the six active British bases. Since the 1959-1960 season, the British have annually chartered a Danish ice-strengthened ship to assist in supply operations. This year, MV *Perla Dan* was chartered, with the principal mission of carrying materials for the complete reconstruction of Halley Bay Base. The Royal Navy ship *Protector* also assists in the resupply, particularly in special projects which require helicopters. The British have no icebreakers, but in the relatively ice-free waters of the Antarctic Peninsula region, the two ice-strengthened ships are usually adequate.

The main features of the current BAS program are detailed hydrographic charting of the waters adjacent to the Antarctic Peninsula and nearby islands, comprehensive meteorological and ionospheric observations, and geological, glaciological, and biological research. The results are disseminated primarily through BAS's own serial publications (*Scientific Reports* and *Bulletins*).

I boarded *Perla Dan* at Montevideo, Uruguay, on December 28, 1966, joining Sir Vivian Fuchs, M. Rolland, and about 25 British personnel, most of whom were bound for Halley Bay Base on the Weddell Sea. Relief personnel for the other five bases had preceded us on *Shackleton* and *John Biscoe*.

Our first stop was made 810 miles south of Montevideo at Port Stanley, capital of the Falkland Islands. Governor and Lady Haskard were our hospitable hosts. There, BAS maintains a permanent field headquarters, with an administrative staff, meteorologists, and a radio-communication center.

The Falklands were once important for provisioning and repairing ships damaged in the stormy waters off Cape Horn, but since the construction of the Panama Canal, most world ship traffic has bypassed the islands. Hulks of many sailing ships are still evident in the Port Stanley harbor. The islands are treeless, grassy, and windswept, providing ideal conditions for rearing sheep, the principal industry.

From the Falklands, we traveled 600 miles across Drake Passage in sunny, calm weather to Deception Island, where Great Britain, Argentina, and Chile maintain year-round bases on the shores of the drowned portion of the crater of the dormant volcano forming the island (Fig. 3). Deception Island is the main base for the small fleet of aircraft maintained by the British. We unloaded a new Swiss-built Pilatus Porter aircraft and brought aboard 21 young dogs which had been bred on the island for use at Halley Bay.

From Deception Island, we steamed 600 miles eastward to the center of British antarctic biological research, Signy Island Base, in the South Orkneys. I left the ship there and stayed for a month, observing the British research programs.

Perla Dan went on to South Georgia, formerly a major whaling station, and then southward across the Weddell Sea to Halley Bay, where a completely new base was under construction. The unloading at Halley Bay was completed just in time: on the day following discharge of the last cargo, the ice shelf began to break up, destroying a natural ice ramp which had provided access to the glacier from the sea each year since the British established the base during the IGY. This year, the Weddell Sea was freer of ice than had been reported in any other year since its discovery in 1823. Owing to this condition, the trip from South Georgia to Halley Bay, which usually takes at least 10 days, was made in 4 days.

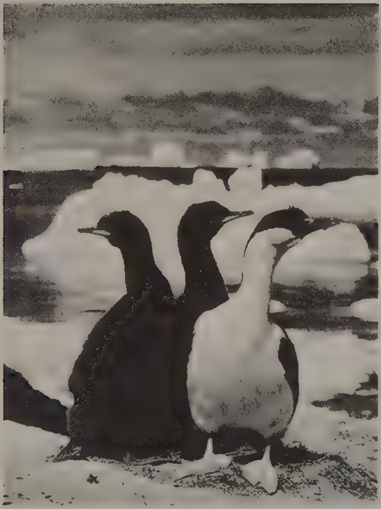

Figure 4. (Left) Blue-eyed shag.

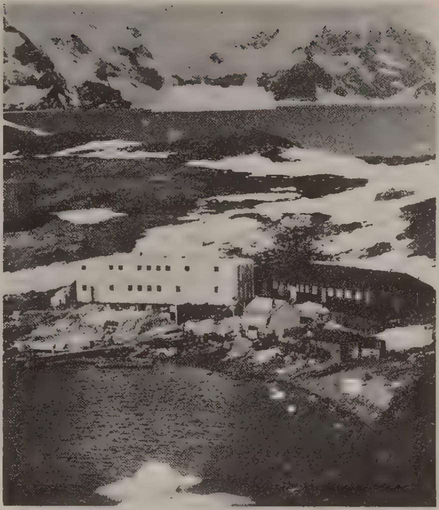

Figure 5. (Right) Signy Island Base with Coronation Island in background. Lower story of fiber glass building has scientific laboratories; living quarters are in upper story. The large black building contains storage rooms and electric generators.

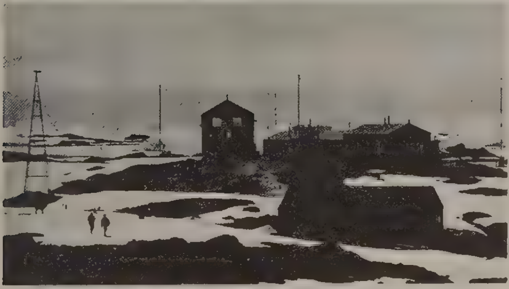

Figure 6. Argentine Islands Base, where extensive meteorological and ionospheric data are collected.

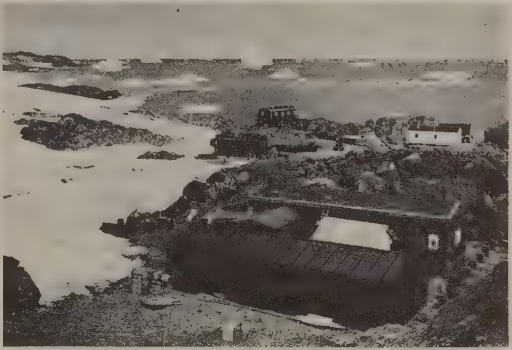

Figure 7. (Above) Adelaide Island Base, the center for British use of light planes.

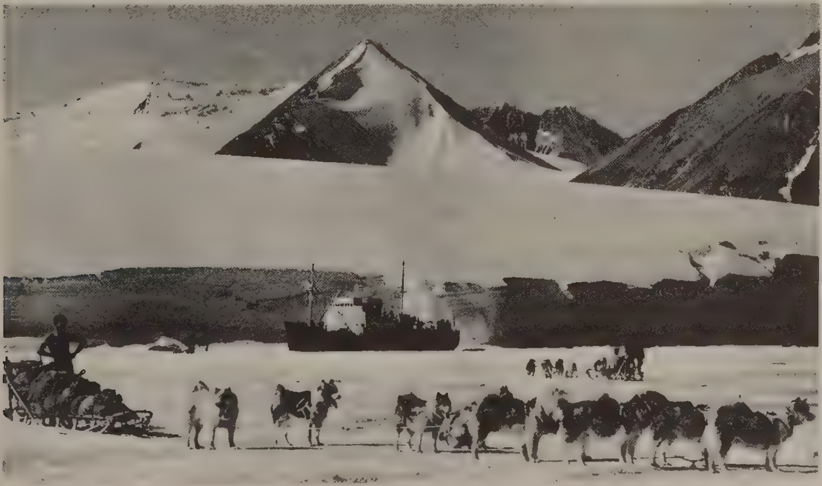

Figure 8. (Left) Moving sacks of coal by dog sled over the fast ice at Stonington Island. Coal is used at most bases for cooking and heating. The glacier in the background serves as a landing field for light planes.

There were 22 men at Signy, about half of whom were scientists (the wintering-over complement numbers about 11). The island offers excellent opportunities for ornithological research because of its large nesting populations of Adélie and chinstrap penguins, skuas, sheathbills, dove prions, and petrels (Wilson's, snow, and giant). Shag are also present (Fig. 4).

The scientists at Signy were an enthusiastic group of well-trained young men who were doing research on a diversity of subjects: cold diuresis in humans; age and growth of lichens; nitrogen fixation by freshwater blue-green algae; breeding habits, ages, and growth rates of the three species of petrels; ecology and life history of the giant isopod *Glyptonotus;* physiology and respiration of the curious "bloodless" fish *Chænichthys;* ecology and blood chemistry of the common antarctic fishes *Notothenia neglecta* and *N. rossi;* chemical adaptation of tissues of *Notothenia* to low temperatures; the effects of soil and air microclimates on the growth of mosses; causes of formation of moss peat; and bacterial characteristics of soil types. Birdbanding was extensive.

The facilities for research at Signy are outstanding (Fig. 5). The main hut is a yellow, double-deck, 30- by 85-foot structure made of bolted-together sections of fiberglass over a layer of insulating foam. This novel building—the first of its kind to be used by the British—proved to be so well adapted to the Antarctic that it has served as the model for most of the new buildings erected at British bases. Such structures cannot be built on ice or snow, however, because uneven settling breaks the joints between sections. The upper story of the Signy hut contains living and eating quarters, and the lower story has about 2,500 square feet of laboratory space. The scientific instruments and supplies are modern and of excellent quality.

My fascinating month at Signy ended when RRS *John Biscoe* returned from Halley Bay in February to finish unloading the year's supplies. From Signy we sailed to King George Island, near the tip of the Antarctic Peninsula, to check the condition of the vacant Admiralty Bay Base. The buildings and equipment were in such good order that little refurbishing will be required to put them in operating condition.

After leaving Admiralty Bay, we rendezvoused with a Royal Navy survey party which was bivouacking on English Strait. Then we returned to Deception Island Base to pick up personnel who had completed one- or two-year tours of duty and were bound for England.

Next, we stopped briefly at tiny Wienke Island to inspect Port Lockroy, another inactive British base, then called at the U.S. Palmer Station on Anvers Island, the site of still another inactive British base. The old British hut is one of two buildings being used by U.S. scientists until the construction of new facilities is completed late in the 1967-1968 austral summer.

From Palmer we headed southward, threading the narrow and beautiful Gerlache Strait, with towering mountains and hanging glaciers on either side of the ship. Near the south end of this strait are the low, rocky, scattered Argentine Islands, on one of which, Galindez Island, is the main antarctic base for British meteorological and ionospheric observations (Fig. 6). This station, at which 12 men work, is a model of efficiency.

The only encounter with pack ice on the entire trip occurred just after crossing the Antarctic Circle, while the ship was en route to the next base, Adelaide Island. A circuitous route took us to the anchorage opposite the base (Fig. 7) in "Iceberg Alley," so-called because of the profusion of bergs which continuously drift back and forth in strong tidal currents. In summer, Adelaide is the center of BAS's air operations. It has two planes, a Pilatus Porter and a de Havilland Otter, which land on an ice piedmont near the base. This year, Dr. Charles Swithinbank of the Scott Polar Research Institute made a survey of the ice thickness of George VI Sound, Alexander Island, Anvers Island, and the Filchner Ice Shelf by means of airborne radio-sounding equipment. This technique, which may revolutionize ice-thickness survey methods, enables three men in a small plane to make a continuous record of ice thickness over hundreds of miles within a few hours.

After leaving Adelaide, we made a brief stop at Stonington Island, the southernmost British base in the peninsula area, and then spent a week hunting seals from *John Briscoe* in "Labeuf Fjord." A large supply of seal meat is needed at Stonington to feed the 80 sledge dogs that transport the mapping and geological-survey parties to and from the field. The British have found that seal meat is the best food available for keeping the dogs in good condition.

During the seal hunt, brief stops were made at two other British bases, Blaiklock Island and Horseshoe Island, which were then inactive but which are used occasionally in winter by sledging parties from Stonington. Both were in excellent condition.

Back at Stonington, we unloaded bags of coal for heating and cooking (Fig. 8), general cargo, and 150 seals, mostly crabeaters. We remained there several days, which enabled me to inspect thoroughly this most picturesque of British bases and to become acquainted with the dozen men stationed there. The base is regarded as one of the most desirable antarctic assignments because of the island's generally clear weather and beautiful scenery and the opportunity provided to participate in long, overland dog-sledging journeys in the style of British heroes of earlier antarctic exploration. Stonington is also of great historic interest since it was the site of the U.S. Antarctic Service's East Base (1939-1941) and Finn Ronne's private U.S. expedition (1947) and because the British have operated their base there intermittently since 1946 (Fig. 9). Some of the U.S. facilities constructed in 1940 are still in remarkably good condition. The original U.S. flagpole is used today by the British, and even the U.S. Weather Bureau instrument shelter, though battered and eroded by blowing snow, still stands atop a boulder.

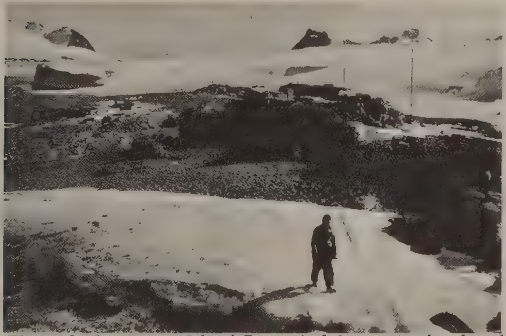

Figure 9. Stonington Island Base. At left rear is abandoned British base, in center foreground is present British base, and in center distance is old East Base. Sir Vivian Fuchs is crossing snowfield.

After completing the resupply of Stonington, we made our return to civilization rapidly and uneventfully, except for an encounter with a screaming Cape Horn gale with mountainous waves 50 feet high and over 200 feet between crests. Sir Vivian Fuchs, M. Rolland, and I debarked at Punta Arenas, Chile, on March 10.

During this resupply operation, the British amply demonstrated that long experience in antarctic exploration and research pays off. All objectives of the complex undertaking were completed as scheduled and without incident, and the programs and facilities were improved at all six bases. Although no scientists from other Antarctic Treaty nations are currently at British bases, the opportunity and incentive for them to work there are sure to increase. The British plan to continue to expand their research programs, especially in biology. Coordinated studies by them and scientists from other countries working on the peninsula would undoubtedly produce great advances in antarctic biology.

During my three months as their guest, the British were unfailingly hospitable, making my visit very productive and pleasant.

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JUVENILE GROWTH OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*

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Oxford, Maryland, and Woods Hole, Massachusetts

(ABSTRACT)

Growth rates of adult scallops, based on shell annuli, have been determined and validated by tagging (Merrill, Posgay, and Nichy 1966). Ring counts cannot be applied however, to scallops smaller than 50 mm since the rings, if present, are poorly defined. Apparently, recognizable rings are first formed at sexual maturity—about 50 mm. When sexual products, which make up one-third of the body weight, develop during late winter and early spring, growth processes are possibly diverted towards gonadal development. The resulting slower growth for the remaining body and shell of the animal produces a ring.

Mean sizes of juvenile sea scallops from natural habitats on the ocean bottom were compared with those from navigation buoys at various times of the year. Growth data were analyzed from 42 collections of small scallops which lived and grew on buoys up to 18 months. Since buoys are on station for known periods of time (Merrill 1965), and the season of spawning is known (Posgay and Norman 1958), information on age is reliable. Scallops from buoys grew, on the average, about 5 mm in 6 months, about 12 mm in 1 year,

and about 20 mm in 18 months. Scallops on the bottom grew faster—to about 25 mm in 18 months. Extrapolation of growth curves, derived from the above data, indicates that scallops grow to about 40 mm in 2 years, become sexually mature and form the first discrete ring in 2½ years, and spawn at the end of that year.

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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

A NEW ARMORED SEAROBIN FISH, *PERISTEDION UNICUSPIS*, FAMILY PERISTEDIIDAE, FROM THE STRAITS OF FLORIDA[1]

By George C. Miller
Tropical Atlantic Biological Laboratory, Miami, Florida

Exploratory fishing on the continental slope of the western North Atlantic by the U. S. Bureau of Commercial Fisheries has shown that armored searobins, *Peristedion* Lacépède, are an important component of the benthic fauna. Presence of three to five species of armored searobins in a single trawl haul is not unusual because the catch may have been made over a wide depth range on a steep slope on several different bottom types. The following catch of peristediids was made in the Straits of Florida off Cay Sal Bank, at *Silver Bay* station 2458: five specimens of *Peristedion antillarum* Teague; one *P. truncatum* (Günther); two *P. longispatha* (Goode and Bean); three *P. greyae* Miller (in press); and two specimens of a fish that I describe here as a new species, distinguished from the closely related *P. longispatha* and *P. greyae*.

The terminology, counts, and measurements follow the methods given by Miller (in press).

Harvey R. Bullis, Jr., made available to me for study the peristediids collected during the operation of the U. S. Bureau of Commercial Fisheries exploratory vessels, *Silver Bay* and *Oregon*, in the western Atlantic. The illustrations are by Grady W. Reinert.

Peristedion unicuspis new species
Cay Sal armored searobin
Figs. 1–3

Diagnosis: Single retrorse spine on posterior scutes of superomedian

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[1] Contribution No. 32, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Florida; and Contribution No. 84, Biological Laboratory, Brunswick, Georgia.

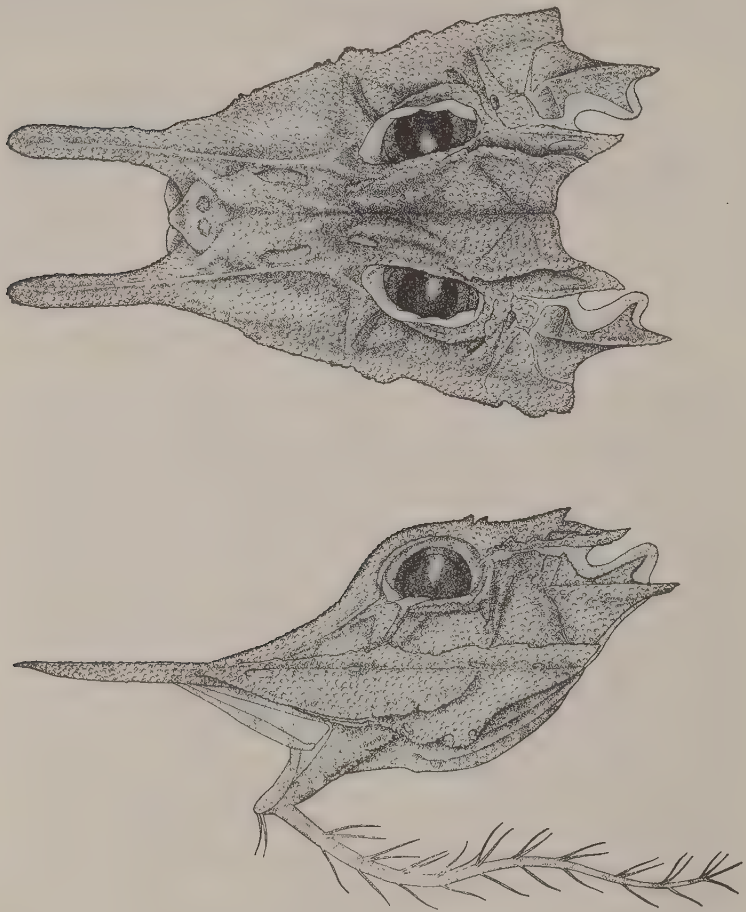

FIG. 1. *Peristedion unicuspis*, holotype. Dorsal and lateral views of head.

series; chin barbels 8 to 9, in 5 groups, arranged 2 + 2 + 2 + 1 + 1 or 2 + 2 + 2 + 2 + 1, on each side of mandibular symphysis; filamentous barbel very long, extending past middle of first ventral scute; first free ray of pectoral long, extending past distal end of pectoral joined rays and anal fin origin; no dark margin on second dorsal fin.

Holotype: USNM 200382, 146 mm standard length (SL), 170 mm total length (TL), collected at *Silver Bay* station 2458, lat. 23°40′N., long. 79°18′W., on 5 November 1960 with a balloon trawl fished at a depth of 290 fathoms.

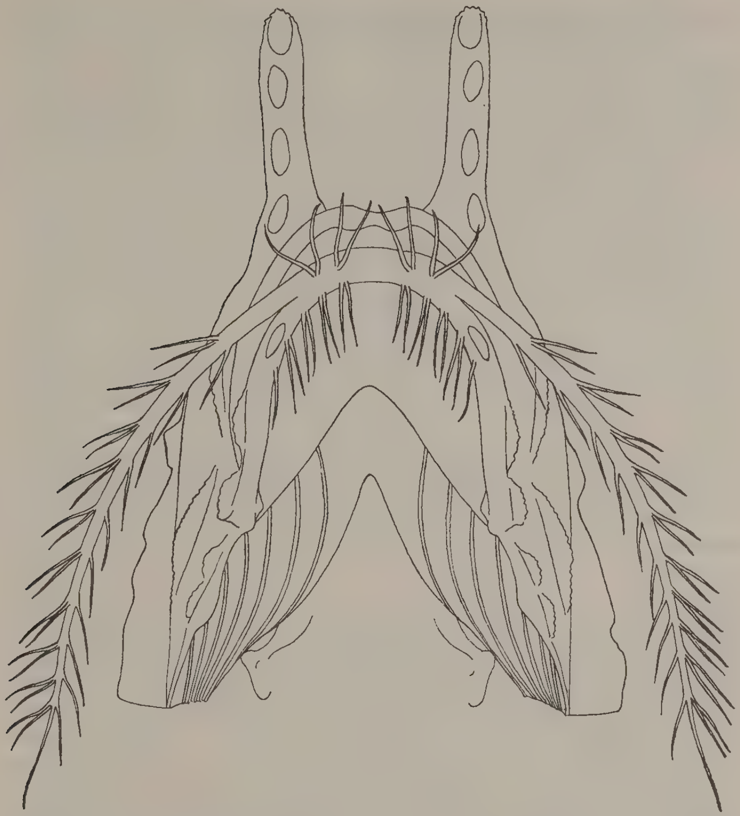

Fig. 2. *Peristedion unicuspis*, holotype. Ventral view of head, showing arrangement of barbels.

Paratype: USNM 200383, 138 mm SL, 157 mm TL; data as for holotype.

Description: Paratype counts are given in parentheses after holotype counts, if they differ.

Dorsal VIII-19 (VIII-20). Anal 20. Pelvic I-5. Pectoral 12 + 2. Lip barbels 4/2 : 4/2. Chin barbels 9/5 : 9/5 (8/5 : 8/5) in the following groups 2 + 2 + 2 + 2 + 1 (2 + 2 + 2 + 1 + 1). Gillrakers first arch: epibranchial 5; ceratobranchial 17; hypobranchial 4; total 26. Vertebrae 33. Branchiostegals 7.

Scutes: dorsal series 25; superomedian series 32; bicuspid spines 0; inferomedian series 24; accessory scutes 3 (2); ventral series 20; caudal series 2-1-2.

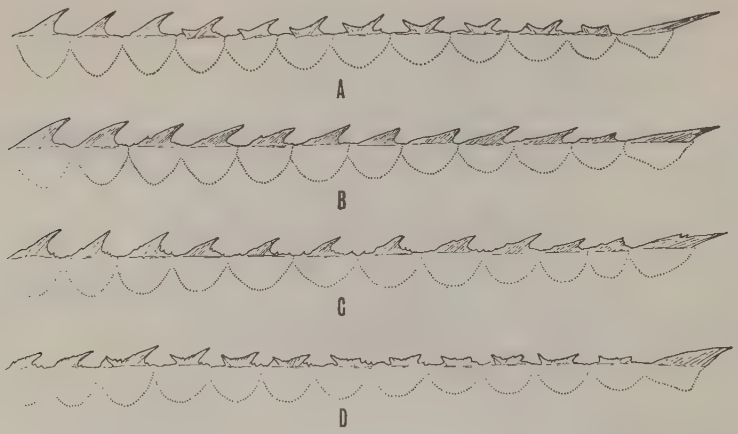

FIG. 3. Comparison of bicuspid spines of scutes of superomedian series: A, *P. greyae* adult (158 mm SL), B, *P. unicuspis* adult (146 mm SL), C, *P. longispatha* adult (158 mm SL), D, *P. longispatha* juvenile (90 mm SL).

Measurements of holotype and paratype in millimeters, expressed in parentheses as percentages of SL. Body depth at first dorsal spine 30.0, 26.5 (20.5, 19.2); at anal fin origin 16.9, 16.0 (11.6, 11.6). Body width at pectoral fin origin 29.8, 25.1 (20.4, 18.2). Head length 55.3, 51.0 (37.9, 37.0). Greatest head width 47.4, 44.5 (32.5, 32.2). Length of joined pectoral fin 27.1, 24.0 (18.6, 17.4). Length of first free pectoral finray 35.3, 30.2 (24.2, 21.9). Length of second free pectoral finray 27.1, 23.9 (18.6, 17.3). Pelvic fin length 25.4, 24.7 (17.4, 17.9).

Measurements of holotype and paratype in millimeters expressed in parentheses as percentages of head length. Filamentous barbel length 51.1, 40.3 (92.4, 79.0). Lip barbel length 6.5, 6.4 (11.8, 12.5). Chin barbel length 4.1, 4.5 (7.4, 8.8). Snout length 26.0, 24.2 (47.0, 47.5), width 21.0, 19.8 (38.0, 38.9). Orbital length 14.3, 13.0 (25.9, 25.5), depth 10.1, 8.1 (18.3, 15.9). Interorbital width 10.8, 10.6 (19.5, 20.8). Rostral exsertion length 19.1, 17.2 (34.5, 33.7); width between rostral exsertions near their bases 11.5, broken on paratype (20.8, –); greatest width of rostral exsertion at base 7.4, 6.9 (13.4, 13.5); width at middle of rostral exsertion 3.8, 3.4 (6.9, 6.7); distance between tips of rostral exsertions 7.2, broken (13.0, –). Distance between parietal spines 9.1, 9.8 (16.5, 19.2). Nape length 7.9, 6.7 (14.3, 13.1). First (posterior) serrated ridge on mandible, length 3.7, 3.9 (6.7, 7.6); width 1.4, 1.1 (2.5, 2.2). Second (anterior) ridge on mandible scarcely discernible, less than 0.2 mm wide. Fourth infraorbital ridge, length 9.1, 7.3 (16.4, 14.3); width 1.4, 0.8 (2.5, 1.6). First ventral scute, length 16.0, 14.0

(29.0, 27.5); width 13.2, 11.4 (23.9, 22.4). Second ventral scute, length 11.5, 10.3 (20.8, 20.2); width 12.6, 10.7 (22.8, 21.0).

Finrays. Pelvic spines smooth, ½ to ¾ length of first pelvic softray; spine translucent; pelvic fin connected to body by membrane between inner pelvic finray and lateral dorsal edge of first ventral scute. First anal finray ½ length of second anal finray. First free pectoral finray long, greatly exceeding length of joined pectoral finrays.

Barbels. Filamentous barbel very long, reaching past middle of first ventral scute with many filaments on barbel. Lip and chin barbels slender, always tapering to point, none ending in enlarged, rounded knob.

Spines and ridges of head. Rostral, nasal, mesethmoid, lateral ethmoid, preocular, supraocular, postocular, and postfrontal spines absent. Frontal I spine very small, 0.4 mm. Frontal II spine small, 1.3 mm, immediately posterior to Frontal I spine (two spines on left side of paratype). Parietal spine small, 3.4 mm, slightly elevated, at posterior termination of parietal ridge; small secondary spine at anterior base of ridge (in paratype ridge, is flat and no secondary spine at anterior end of ridge). Pterotic spine small, 0.3 mm, on nearly obsolete ridge. Posttemporal spine blunt, small, 1.3 mm, at termination of long, low 8.2-mm straight ridge. Opercle spine small, with distal end bicuspid (unicuspid in paratype), at posterior end of 12.4-mm serrated opercular ridge. Perifacial rim: on second infraorbital, narrow, with two small spines followed by a slightly rounded protuberance; on third infraorbital, three separated sharp spines followed by a rounded protuberance with serrated edge; on preopercle, strong concavity posterior to orbit on left side, none on right side; three to five slight indentations on perifacial rim of holotype and paratype; ending posteriorly as wide shelf with posterior edge perpendicular to head. On second infraorbital, three very narrow ridges extending from corner of mouth to second infraorbital spines, nearly parallel to each other and to premaxillary, mouth closed. On fourth infraorbital, pronounced ridge beneath eye extending posteroventrad. On preopercle, dorsal ridge long, narrow, from corner of mouth posterodorsad, terminating below sensory organ on perifacial rim; anterior ventral ridge small, near edge of, and on preopercle, immediately behind posterior ridge of mandible; posterior ventral ridge small, on ventral edge of preopercle with two openings of preoperculo-mandibular canal on either side of ridge. On mandible, first posterior ridge strong, serrated; second ridge short, narrow, anterior to first ridge on left side, but absent on right side (absent in paratype). Rostral exsertions of moderate length, 19.1 mm, and width at the base 7.4 mm; in normal position slightly divergent; nearly equal in width from rounded distal ends to base; lacking prominent serrations on distal ends.

Spines and scutes of body. Nuchal spine present, 3.0 mm, approximately ½ size of first spine of dorsal series; small spine at anterior edge of nuchal ridge (lacking in paratype). Dorsal series: strong, sharp spines on dorsal scutes, becoming slightly smaller posteriorly. Superomedian series: first scute at anterior end of arch bearing ridge terminating in small tubercle; scutes two, three, and four of arch may have large, sharp spines on ridges; spines strong, sharp, decreasing little in size posteriorly; few spines on posterior eight or nine scutes have extremely small anterior retrorse spines at bases, possibly indicating these spines may be bicuspid in young; superomedian spines located closer to dorsal spines than to inferomedian spines. Inferomedian series: inferomedian scute row arches ventrally immediately posterior to accessory scutes; small retrorse spine at anterior edge of base of main spine (not evident on paratype); posterior two scutes ventral to others in series, without small anterior retrorse spines; all main spines in series strong. Accessory scutes: three scutes between inferomedian and ventral series (two scutes in paratype). Ventral series: first ventral scute with obsolete spine, second with tubercle, third with small spine, fourth with large spine, size of succeeding spines decreasing posteriorly to small tubercle on scute at last anal ray; anterior edge of first ventral scute posterior to bony ridge of pelvic girdle (bony ridge visible beneath skin). Caudal series: two dorsal, one lateral, and two ventral scutes; edges of caudal spines smooth; distal end of lateral caudal spine extending posteriorly as far as ends of dorsal and ventral caudal spines.

Pigmentation. Body and head pale grey. Distal half of membrane between anterior five dorsal spines black. A few small, black pigment spots scattered sparsely on soft dorsal fin rays, no dark margin. Small black spot scarcely visible at middle of pale grey pectoral. Posterior portion of roof of mouth dusky. Peritoneum and air bladder membrane dusky.

Etymology: The species name *unicuspis*, derived from Latin—*unus* meaning one, and *cuspis* meaning point (named for the single, retrorse spine found on each posterior scute of the superomedian series of the adults), is regarded as a noun in apposition to the generic name. The species is given the common name, Cay Sal armored searobin, for the locality of capture.

Relationship: The two species most closely related to *P. unicuspis* are *P. greyae* and *P. longispatha*. These three species may be distinguished as follows:

1a. Two or three prominent, strong, serrated ridges on mandible; filamentous barbel moderately long, not reaching termination of perifacial rim; lip barbel half-counts 4/2, grouped 2 + 2; chin barbel half-counts 12–13/5, usually grouped 3 + 3 + 3 + 2 + 1 or 3 + 3 + 3 + 2 + 2; barbel tips pointed; rostral exsertion spine present, nasal spine absent; biscuspid spines present in young and adults; accessory scutes present or absent; distal one-third of pectoral fin dark; wide, dark margin on soft dorsal fin; peritoneum and posterior portion of roof of mouth translucent .. *P. greyae* Miller

1b. One prominent, strong, serrated ridge on mandible 2

2a. Filamentous barbel very long, extending past termination of perifacial rim to posterior one-half of first ventral scute; lip barbel half-counts 4/2, grouped 2 + 2; chin barbel half-counts 8–9/5 grouped 2 + 2 + 2 + 1 + 1 or 2 + 2 + 2 + 2 + 1; barbel tips pointed; rostral exsertion spine and nasal spine absent in adults; bicuspid spines absent in adults; accessory scutes present; pectoral fin with single small, dark spot at center; lacking dark margin on soft dorsal fin; peritoneum and posterior portion of roof of mouth dusky .... *P. unicuspis* Miller

2b. Filamentous barbel moderately long, not reaching termination of perifacial rim; lip barbel half-counts 2/2, grouped 1 + 1; chin barbel half-counts 11–14/6, usually grouped 1 + 2 + 3 + 3 + 2 + 2 or 1 + 2 + 2 + 3 + 2 + 2; barbels generally with enlarged, rounded tips; rostral exsertion spine and nasal spine present in juveniles, absent in large adults; bicuspid spines or vestiges, present in juveniles and adults; accessory scutes absent; pectoral dusky; dark margin on soft dorsal fin; peritoneum and posterior portion of roof of mouth translucent .... *P. longispatha* (Goode and Bean)

I have found ontogenetic differences in the bicuspid spines of *P. greyae, P. longispatha,* and *P. unicuspis.* In *P. greyae,* bicuspid spines in the posterior portion of the superomedian series were present in both the smallest and largest specimens examined. The number of bicuspid spines in the young of *P. longispatha* decreases and the number of unicuspid spines increases with growth of the fish. Loss of the small anterior cusp of the spine occurs first on anterior scutes and proceeds posteriorly. The small anterior cusp of the bicuspid spine in *P. longispatha* may be connected to the body by a membrane, making the bicuspid spine appear to be unicuspid. I speculate that young *P. unicuspis* also may bear bicuspid spines. The posterior superomedian scutes and the lateral caudal scutes of the three adults and one juvenile of these closely related species are shown in Fig. 3.

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A NEW SPECIES OF WESTERN ATLANTIC ARMORED SEAROBIN, *PERISTEDION GREYAE* (PISCES: PERISTEDIIDAE)

GEORGE C. MILLER

A NEW SPECIES OF WESTERN ATLANTIC ARMORED SEAROBIN, *PERISTEDION GREYAE* (PISCES: PERISTEDIIDAE)[1]

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ABSTRACT

A new species of armored searobin, *Peristedion*, from the western Atlantic Ocean is described. It is distinguished from *P. antillarum* in having more numerous lip and chin barbels, shorter and broader rostral exsertions, and a spinous, serrated perifacial rim, and from all other western Atlantic species in having two or three serrated ridges on the mandible. Methods and terminology are revised and clarified. Taxonomic problems resolved are: *Acanthostedion* = *Satyrichthys*, *Peristedion spiniger* = *P. truncatum*, *P. bartschi* = *P. longispatha*, *P. taeniopterum* = *P. gracile*, *P. mcgintyi* = *P. miniatum*, and *P. schmitti* = *P. thompsoni*. "Acanthostedion" is proposed to describe the postlarval stages of peristediids. *P. ecuadorensis* does not occur in the Pacific; its type locality is corrected to the western Atlantic.

INTRODUCTION

During exploratory fishing, the U. S. Fish and Wildlife Service vessels caught many armored searobins, *Peristedion* Lacépède, 1802, in the western North Atlantic. Study of the vast amount of new material led me to differ with the conclusion drawn by Teague (1961). The most common species of *Peristedion* collected in the western Atlantic, formerly identified as *P. longispatha* (Goode & Bean, 1886) using existing artificial keys to the species, is here described as a new species.

A brief discussion of the ontogenetic changes between postlarval and juvenile stages is necessary because specimens in these stages have been described as nominal species. The larvae of *Peristedion* are pelagic, metamorphosing into postlarvae before they become benthic juveniles. The postlarvae may be distinguished by their long parietal spines (= occipital spines of Fowler, 1943:76), short, developing rostral exsertions, and incomplete development of the scutes. The postlarva of some species may not metamorphose until between 40 and 60 mm standard length (SL). Teague (1961) apparently was unaware of this metamorphosis, as he failed to comment on three of Fowler's (1952) western Atlantic species, *Peristedion mcgintyi*, *P. thompsoni*, and *P. taeniopterum*, two named from postlarvae and one from a small juvenile. In examining types of these species I found that *P. mcgintyi* is a postlarval form and a junior synonym of *P. miniatum* (Goode, 1880), based on the distinctive perifacial rim and the 3+2+2+2:3+2+2+2 chin barbel counts of the paratypes; *P. taeniopterum* is a small juvenile and junior synonym of *P. gracile* Goode & Bean, 1896 based on the long, very narrow dorsal ridge of the preopercle; and *P. thompsoni*, a postlarval stage, is a senior synonym, and *P. schmitti* Teague, 1961, a junior synonym, on the basis of the perifacial rim terminating in an elongated flat spine, having low inferomedian scute counts (20-21), lacking nasal spines (present in postlarvae of *P. platycephalum* (Goode & Bean, 1886)), and having a small accessory spine at the posterior termination of the perifacial rim.

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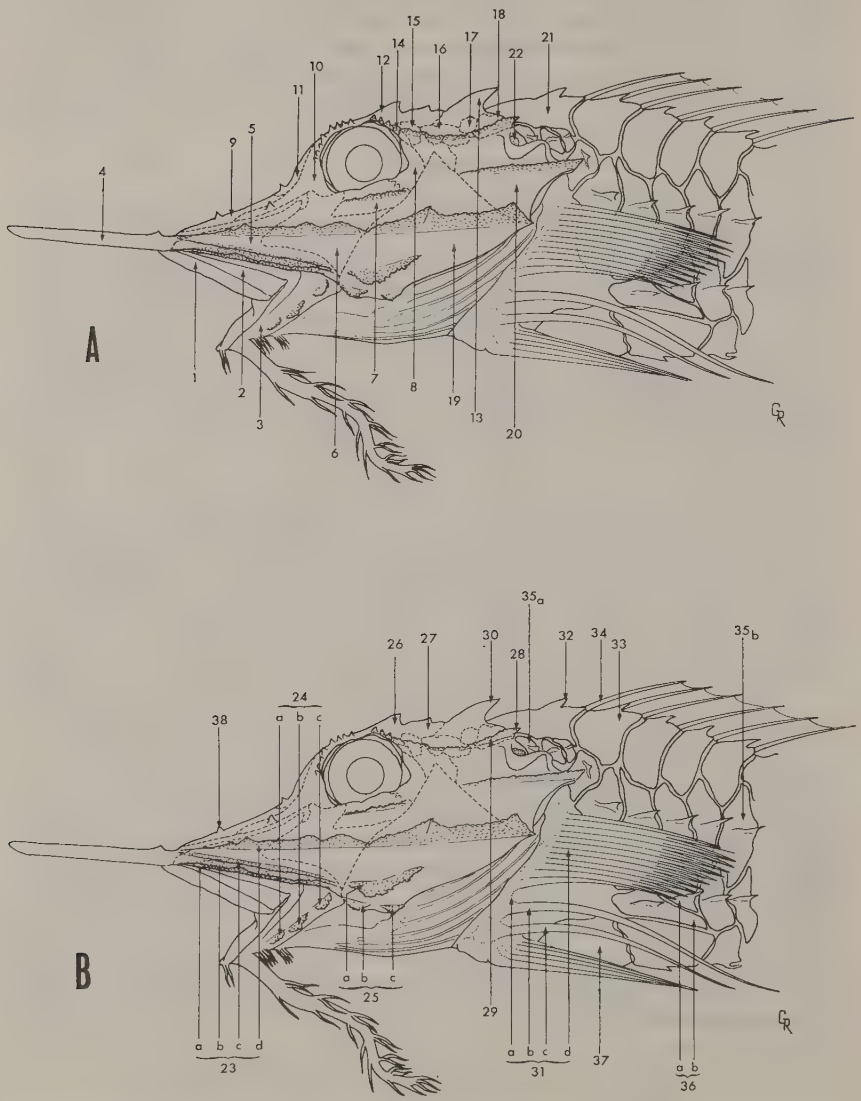
[1] Contribution No. 45 from the U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida, and Contribution No. 84 from the Biological Laboratory, Brunswick, Georgia.

I determined that the description of *Acanthostedion* Fowler, 1943, is based on postlarvae and juveniles, and that the genus is congeneric with *Satyrichthys* Kaup, 1873. The five dorsal spines designated for the genotype, *Acanthostedion rugosum* Fowler, 1943 (USNM 99501), was based upon a damaged specimen; three paratypes (USNM 99502) which I examined had seven dorsal spines. I propose that the name "acanthostedion" be applied to the postlarval stage of peristediids having long parietal spines and developing rostral exsertions, and that this stage is comparable to the "tholichthys" stage of the Chaetodontidae, the "acronurus" of the Acanthuridae, and the "rhynchichthys" of the Holocentridae.

I thank the following persons for the loan or examination of specimens, and helpful criticisms and suggestions: Giles W. Mead and Myvanwy M. Dick, Museum of Comparative Zoology; Leonard P. Schultz, Stanley H. Weitzman, and Robert H. Kanazawa, U. S. National Museum; G. Palmer, British Museum (Natural History); Loren P. Woods and Pearl M. Sonoda, Chicago Natural History Museum; Gordon Gunter and Charles E. Dawson, Gulf Coast Research Laboratory; Royal D. Suttkus, Tulane University; George S. Myers and Alan E. Leviton, Stanford University; C. Richard Robins and William N. Eschmeyer, Institute of Marine Science, University of Miami; Daniel M. Cohen and Bruce B. Collette, Bureau of Commercial Fisheries Ichthyological Laboratory, Washington, D. C.; William J. Richards, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida; and to Walter R. Courtenay, Jr., Boston University. I am particularly indebted to Harvey R. Bullis, Jr., Director of the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base at Pascagoula, Mississippi, for the wealth of material presented to me for study. The illustrations are by Grady W. Reinert. The major portion of the study was completed at the Biological Laboratory, Brunswick, Georgia.

METHODS, TERMINOLOGY, AND ABBREVIATIONS

Procedure.—I found that meristic and morphometric data in many peristediid type descriptions were incomparable because the terminology and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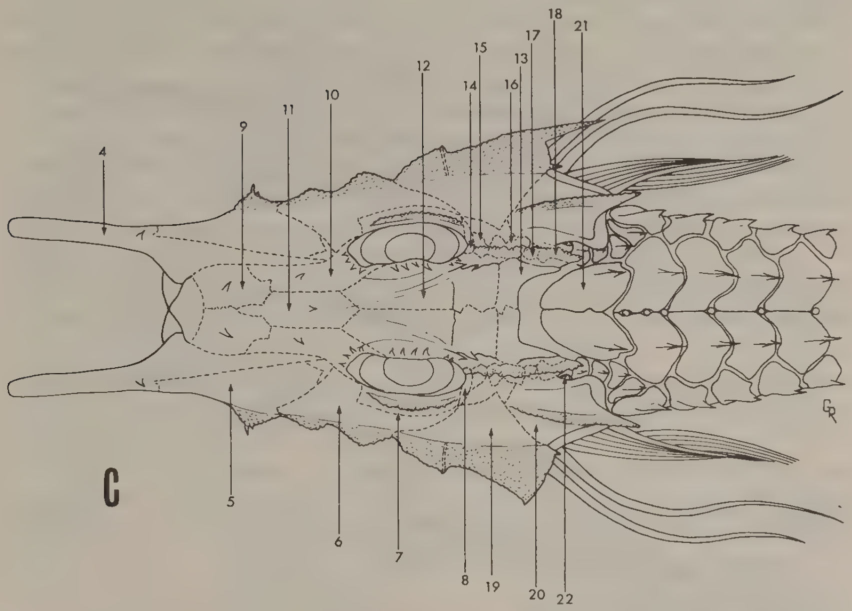

FIGURE 1. Dorsal and lateral views of head and anterior portion of body of a peristediid, showing bones, scutes, and diagnostic characters.

1. Premaxillary
2. Maxillary
3. Mandible
4. Rostral exsertion
5. 2nd infraorbital
6. 3rd infraorbital
7. 4th infraorbital
8. 5th infraorbital
9. Nasal
10. Lateral ethmoid
11. Mesethmoid
12. Frontal
13. Parietal
14. Sphenotic
15. Dermosphenotic
16. Pterotic
17. Extrascapular
18. Post-temporal
19. Preopercle
20. Opercle
21. Nuchal scute
22. Supracleithrum
23. 2nd infraorbital ridges
    a. 1st ridge
    b. 2nd ridge
    c. 3rd ridge
    d. perifacial rim
24. Mandibular ridges
    a. 3rd ridge
    b. 2nd ridge
    c. 1st ridge
25. Preopercular ridges
    a. dorsal ridge
    b. anterior ventral ridge
    c. posterior ventral ridge
26. Frontal I spine
27. Frontal II spine
28. Post-temporal spine
29. Post-temporal ridge
30. Parietal spine
31. Pectoral fin
    a. apex of joined rays with free rays
    b. 1st free ray
    c. 2nd free ray
    d. joined rays
32. Nuchal spine
33. Dorsal series, 1st scute
34. 1st dorsal spine
35. Superomedian series
    a. 1st scute
    b. 9th scute
36. Inferomedian series
    a. 1st scute
    b. Accessory scute
37. Ventral series, 1st scute
38. Nasal spine

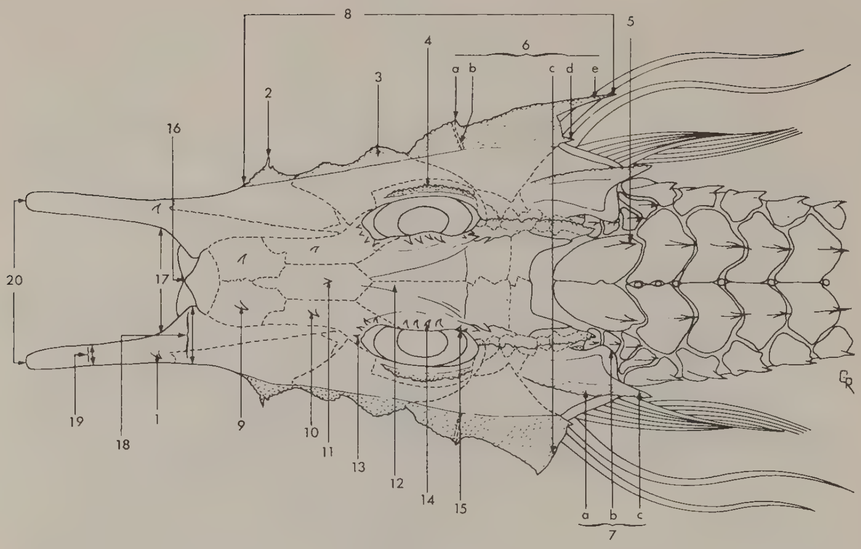

FIGURE 2. Dorsal view of head and anterior portion of body of a peristediid, showing additional diagnostic characters.

1. Rostral exsertion spine
2. 2nd infraorbital spine
3. 3rd infraorbital perifacial rim
4. 4th infraorbital ridge
5. Nuchal spine
6. Preopercular
   a. remnant spine
   b. sensory canal in perifacial rim
   c. perifacial rim termination as flat shelf
   d. accessory spine
   e. perifacial rim termination as spine
7. Opercular
   a. ridge
   b. posterior-most point of flexible margin
   c. spine
8. Perifacial rim
9. Nasal spine
10. Lateral ethmoid spine
11. Mesethmoid spine
12. Interorbital frontal depression
13. Preocular spines
14. Supraocular spines
15. Postocular spines
16. Premaxillary symphysis
17. Distance between rostral exsertions, near base
18. Greatest width of rostral exsertion
19. Width of rostral exsertion at middle
20. Distance between tips of rostral exsertions

methods used were not defined. The anatomical characters I used are shown in Figures 1 to 4.

Teague (1961) compared the species of *Peristedion* in the western Atlantic using well-defined procedures. I follow his methods and terminology, with some exceptions, as discussed in the following sections.

Useful Diagnostic Characters.—In examining specimens of over half of the nominal species of peristediids, the following characters were particularly useful in distinguishing species: lengths of joined and free rays of pectoral fin relative to head length; mandibular barbel length and the type and length of its filaments; number of lip and chin barbels and number of barbel groups; shape and length of gillrakers; shape of head and body; shape, size, and location of spines and bony ridges on head; shape, type of posterior termination, and number and size of spines of the perifacial rim; shape of rostral exsertion; number and shape of sensory pores on rostral exsertions; orbital length and width, and interorbital width; snout length and least width; shape and number of scutes in the four body series; position of anterior edge of first (anterior) ventral scute relative to anterior bony edge of pelvic girdle; location of the anus; shape and striations of first and second ventral scutes; and presence or absence of mid-dorsal groove between dorsal and caudal fins, and midventral groove between anal and caudal fin.

Meristics.—PECTORAL AND PELVIC RAY COUNTS: Counts, determined by dissection, were made on the left side of 50 specimens from R/V SILVER BAY sta. 4227, but not on type material.

CAUDAL RAY COUNTS: Counts, from alizarin-stained caudal fins of 21 specimens (SILVER BAY sta. 4227), are presented as dorsal secondary rays plus dorsal principal rays plus ventral principal rays plus ventral secondary rays. The principal rays articulate with the hypural plates; the secondary rays do not.

LIP AND CHIN BARBEL COUNTS: I indicate the lip and the chin barbels on the left and right side of the symphysis of the mandible as the total number of barbels divided by the number of groups in which they occur. In the example 12/5:13/6, the colon represents the separation of the left and right side, numbers to left and right of the sign refer to counts made respectively from left and right side of the fish in ventral view, 12 and 13 are numbers of chin barbels on left and right side, and 5 and 6 are numbers of groups in which the barbels occur. Variation is limited in the number of barbels in groups occupying similar positions on different fish. The new species described herein usually has its barbels arranged in the following grouping from anterior to posterior or laterally on both sides of the symphysis: chin barbels, 3+3+3+2+1:3+3+3+2+1 expressed as 12/5:12/5; and lip barbels, 2+2:2+2, expressed as 4/2:4/2 (Figs. 3, 6). The number and location of barbel groups and the number of barbels in the group are nearly bilaterally symmetrical. Because of this symmetry, chin barbels were grouped in half-counts to show the range within a species (Table 3). The number of filaments on the filamentous barbel is diagnostic in some species. In the eastern Pacific species *Peristedion barbiger* (Garman, 1899), it is difficult to distinguish between lip and chin barbels because some lip barbels are on the posterior edge of the lip. Barbels may be seen easily and counted accurately with transmitted light.

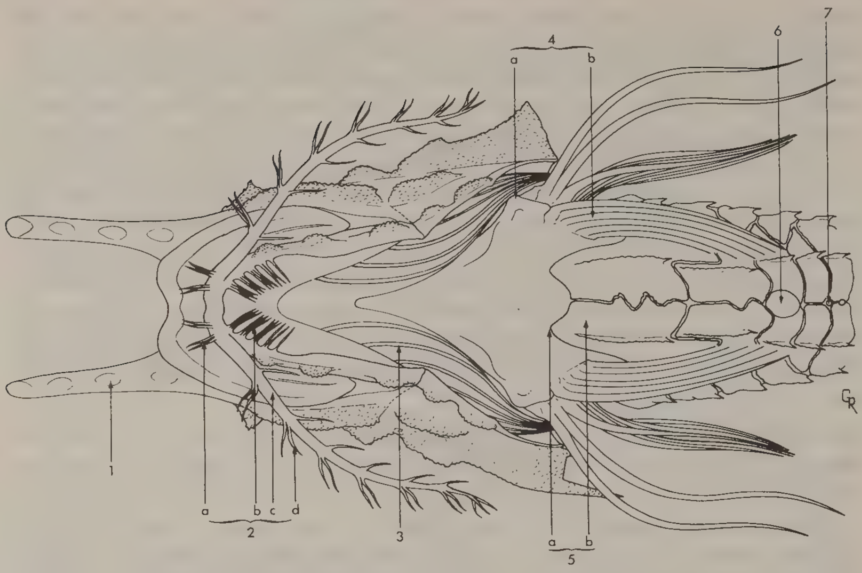

FIGURE 3. Ventral view of head and anterior portion of body of a peristediid, showing additional diagnostic characters.

1. Sensory pore
2. Barbels
   a. lip
   b. chin
   c. filamentous
   d. filaments on filamentous barbel
3. Branchiostegal
4. a. Pelvic girdle, anterior edge
   b. Pelvic fin
5. Ventral series
   a. 1st scute, anterior edge
   b. 1st scute
6. Anus
7. 1st anal ray

GILLRAKER COUNTS: Counts are from 60 type, and an additional 40, specimens. Gillrakers, including tubercles, are counted on the epibranchial, ceratobranchial, and hypobranchial portions of the right side of the first arch; the slender raker at the junction of the epibranchial and ceratobranchial is included in the count for the ceratobranchial.

BRANCHIOSTEGAL COUNTS: Counts of branchiostegal rays are from the left side of 25 dissected specimens (SILVER BAY sta. 4227), but not from type material.

SCUTE COUNTS: Counts were usually made on the left side. Dorsal series (first row), superomedian series (second row), inferomedian series (third row), and ventral series (fourth row), include all scutes in each series (Figs. 1-4). Superomedian series: the first scute-like, serrated structure on the dorsal surface of the supracleithrum is not included (Fig. 1A, No. 22); usually four, sometimes five, scutes on the anterior arch of this series; bicuspid spine counts include all bicuspid spines on the posterior scutes in the superomedian series, including the last one or two scutes, whether they bear unicuspid or bicuspid spines. Inferomedian series: I arbitrarily included in the inferomedian series the posterior two or three scutes which coalesced with adjacent scutes in the ventral series; accessory scutes (infraserial bifurcating scutes of Teague) that may occur anteriorly between the inferomedian series and the ventral series are not included in the inferomedian series. Ventral series: Teague (1961:2) distinguished the abdominal keeled scutes from the other ventral scutes, but I found this separation valueless; the last discernible ventral scute in most Atlantic peristediids usually occurs at the posterior anal ray. Caudal series: all peristediids examined had two dorsal and two ventral scutes on the caudal fin base and one lateral scute; these are listed as 2-1-2.

Measurements.—The following lengths were measured from the premaxillary symphysis: total length, to distal end of caudal rays; standard length, to posterior edge of hypural plate; head length, to posterior lateral flexible edge of opercle; snout (rostral) length, to anterior bony rim of orbit (minimum length); rostral exsertion length, to anterior end of rostral exsertions. Lengths of joined pectoral rays and first and second free ray (first free ray adjacent to ventral portion of pectoral fin), from apex of ventral most joined ray and first free ray (Fig. 1B, No. 31a) to tip of respective ray; pelvic fin length, from base of median ray to tip of pelvic fin. Rostral exsertions: distance between rostral exsertions near base, measured between apex of angles as exsertions broaden posteriorly (Fig. 2, No. 17); distance between rostral exsertions at tips, between distal median margins of exsertions (Fig. 2, No. 20); greatest width, at base immediately posterior to premaxillary symphysis (Fig. 2, No. 18); width of rostral exsertion at middle, measured at one-half the distance between the distal end and the angle the exsertion makes posteriorly (Fig. 2, No. 19). Orbital length: greatest horizontal distance between bony rims of orbit. Orbital depth: greatest vertical distance between bony rims of orbit. Nape length: posterior dorsal median edge of skull to interorbital frontal depression. Spines and tubercles: distal end to anterior edge of base; if spine located at posterior end and continuation of inclined ridge, measurement is from tip of spine to anterior origin of ridge; distance between parietal spine, measurement between tips of spines. First and second ventral scute length, greatest dimension: first and second scute width, greatest width of ventral portion of scute.

The measurements used by Teague (1961) were divided into head length and standard length, whereas I present them as percentages of head length and standard length.

Cranial Anatomy.—Teague (1961:Text Fig. 1) labeled the spines and

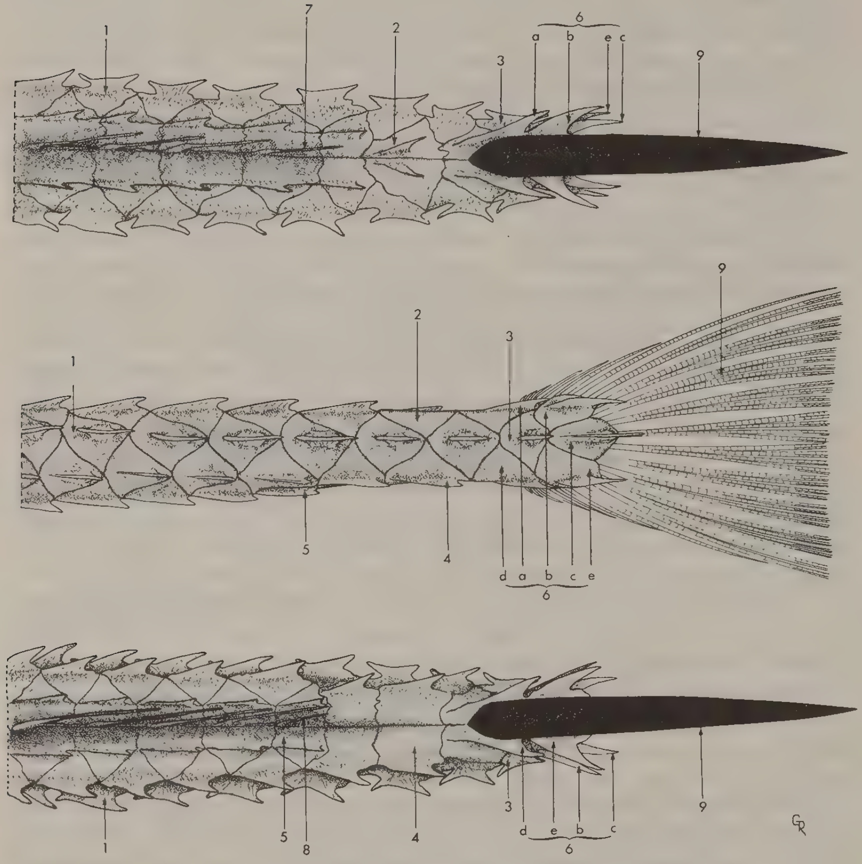

FIGURE 4. Dorsal (upper), lateral (middle), and ventral (lower) views of caudal region of a peristediid, showing diagnostic characters.

1. Bicuspid spine, 1st scute
2. Dorsal series, last scute
3. Superomedian series and bicuspid spine, last scute
4. Inferomedian series, last scute
5. Ventral series, last scute
6. Caudal series
    a. anterior dorsal scute
    b. posterior dorsal scute
    c. lateral scute
    d. anterior ventral scute
    e. posterior ventral scute
7. Last dorsal ray
8. Last anal ray
9. Caudal fin

ridges in a composite cranial diagram. One of these names, "third suborbital," refers to a ridge on the preopercle. I designate this ridge the dorsal preopercular ridge (Fig. 1B, No. 25a).

The shape and sutures of the cranial bones of the new species of *Peristedion* described herein are similar to those of *P. cataphractum* (Linnaeus, 1758) which were accurately described and illustrated by Allis (1909:136-156, Pl. 6) in his excellent description of the cranial anatomy of the mail-cheeked fishes, order Scleroparei. I follow Allis' terminology, except for several names now commonly used, as suggested by Stanley H. Weitzman (personal communication).

The spines, ridges, and bones of diagnostic use are shown in the composite diagrams of a peristediid (Figs. 1-4). Spines and ridges that require explanation are defined as follows: postocular spines, along posterior lateral edge of bony rim of orbit on frontals; frontal I spine, on frontal ridge above posterior bony rim of orbit; frontal II spine, spines, or ridge on frontal bone a short distance behind frontal I spine and in line with parietal ridge; post-temporal ridge or small ridges, on the small bones of sphenotic, dermosphenotic, pterotic, extrascapular, and post-temporals immediately above the opercle, preopercle, and fifth infraorbital; perifacial rim, lateral, elongated ridge, which may extend from base of the rostral exsertions to the posterior edge of the preopercle. The locations of some of the primary sense organs of the head of the holotype are depicted in Figures 5 and 6, but the organs are not described herein.

Abbreviations.—The names of the museums and other sources from which materials were obtained or in which type material was deposited are abbreviated as follows: AM, Australian Museum, Sydney; ANSP, Academy of Natural Sciences of Philadelphia; BLBG, U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia; BMNH, British Museum (Natural History), London; BOC, Bingham Oceanographic Collections, Yale University; CNHM, Chicago Natural History Museum; CU, Division of Biological Sciences, Cornell University; FSBC, Florida State Board of Conservation, St. Petersburg; GCRL, Gulf Coast Research Laboratory; IM, Indian Museum, Calcutta; IRSNB, Institute Royal des Sciences Naturelles de Belge, Brussels; LMNH, Rijksmuseum van Natuurlijke Historie; MCZ, Museum of Comparative Zoology, Harvard University; MN, Naturalista do Museu Nacional, Rio de Janeiro; MNHN, Muséum National d'Histoire Naturelle, Paris; SU, Division of Systematic Biology, Stanford University; TABL, U. S. Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida; TU, Tulane University; UMML, University of Miami Marine Laboratory; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum; UW, University of Washington College of Fisheries.

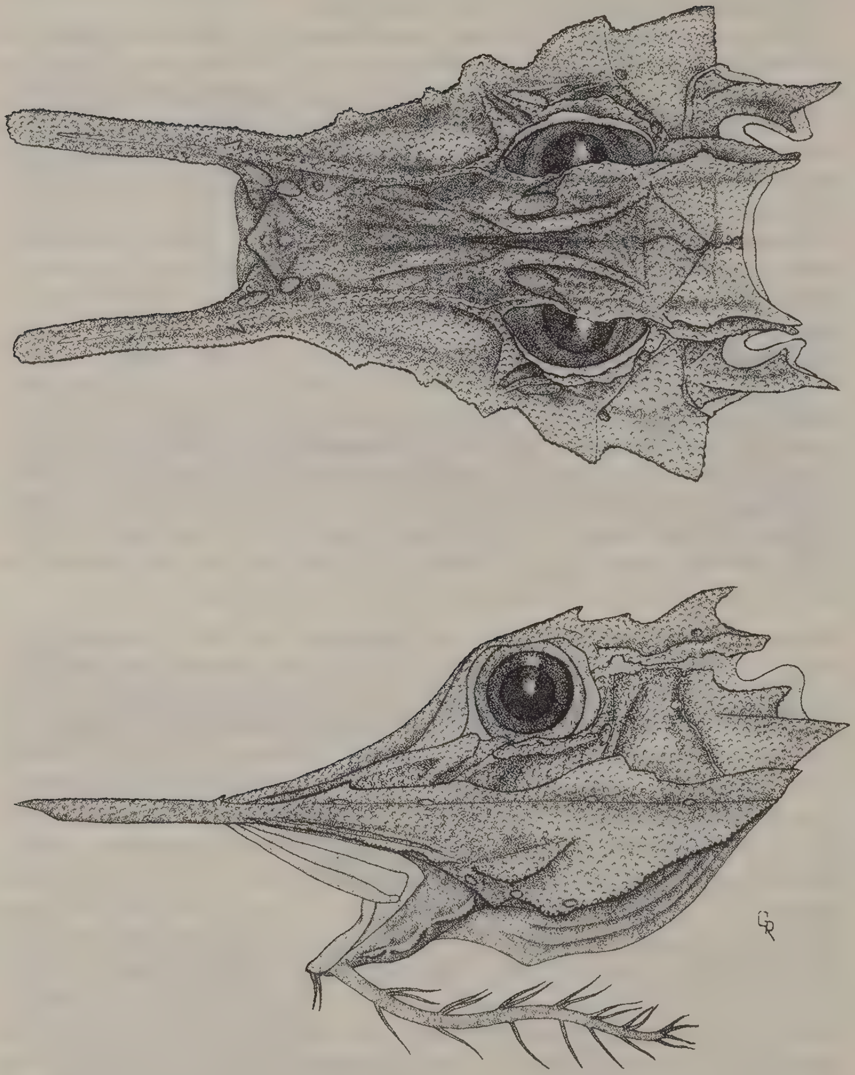

FIGURE 5. *Peristedion greyae*, holotype, USNM 198124. Dorsal and lateral view of head.

Peristedion greyae, new species

PRICKLY ARMORED SEAROBIN

Figs. 5, 6; Tables 1-3

Peristedium longispatha (*non* Goode & Bean, 1886), Goode & Bean, 1886: 167 (in part; ALBATROSS sta. 2376 & 2397).

Peristedion longispatha (*non* Goode & Bean, 1886), Goode & Bean, 1896: 472 (in part; ALBATROSS sta. 2376 & 2397, and coloration notes).—Myers, 1934: 12 (comparison of *P. bartschi* Myers, 1934 with specimens synonymous with *P. greyae*).

Peristedion longispathum (*non* Goode & Bean, 1886), Jordan & Evermann, 1898: 2178-2179 (in part; ALBATROSS sta. 2376 & 2397).—Evermann & Marsh, 1900: 284 (in part; ALBATROSS sta. 2376 & 2397).—Longley & Hildebrand, 1941: 169 (meristics and morphometrics of specimens synonymous with *P. greyae*).—Teague, 1961: 13-14 (in part; USNM 117051 and USNM 210952, meristics and morphometrics partially those of specimens synonymous with *P. greyae*).

Diagnosis.—Two or three separate and distinct serrated ridges on mandible; if present, third ridge generally very low, and barely perceptible. Usually a strong concavity on outer edge of perifacial rim of preopercle. Rostral exsertion spine generally present. Chin barbel counts predominantly12-13/5:12-13/5 with the barbels usually arranged in the following groupings, 3+3+3+2+1 or 3+3+3+2+2.

Description of the Holotype.—Standard length 132 mm. Total length 152 mm. Dorsal fin-ray count VIII-19. Anal fin rays 21. Pelvic fin rays I-5. Pectoral fin rays 12+2. Lip barbels 4/2:4/2; chin barbels 12/5:12/5. Gillrakers on first arch: epibranchial 6; ceratobranchial 18; hypobranchial 4; total 28. Rostral exsertion spine 1. Serrated ridges on mandible 3. Vertebrae 35. Branchiostegals 7. Scutes: dorsal series 27; superomedian series 33, bicuspid spines 11; accessory scutes 0; inferomedian series 25; ventral series 24; caudal series 2+1+2.

Measurement in millimeters with percentage of standard length in parentheses. Body depth at first dorsal spine 25.7 (19.5); at anal-fin origin 17.0 (12.9). Body width at pectoral fin origin 21.5 (16.3). Head length 47.8 (36.2). Greatest head width 40.6 (30.8). Length of joined pectoral finray 23.0 (17.4). Length of first free pectoral finray 27.9 (21.1). Length of second free pectoral finray 23.0 (17.4). Pelvic finray length 28.5 (21.6).

Measurement in millimeters with percentage of head length in parentheses. Filamentous barbel length 21.1 (44.1). Lip barbel length 4.3 (9.0). Chin barbel length 3.6 (7.5). Snout length 21.3 (44.6), width 16.2 (33.9). Orbital length 12.0 (25.1), depth 8.3 (17.4). Interorbital width 9.7 (20.3). Rostral exsertion length 17.4 (36.4); distance between rostral exsertions near base 9.9 (20.7); greatest width of rostral exsertion at base 5.6 (11.7); width at middle of rostral exsertion 3.1 (6.5); distance between rostral exsertions at tips 15.7 (32.8). Distance between

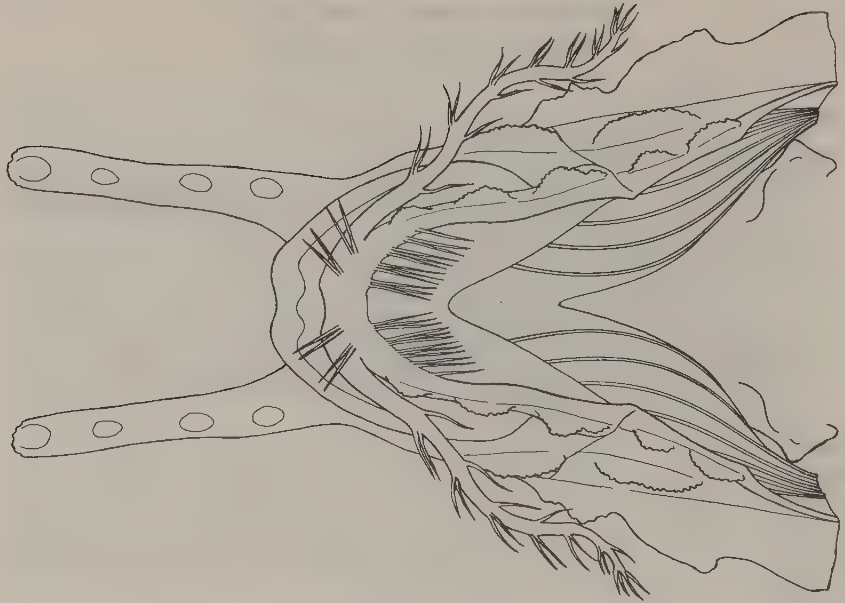

FIGURE 6. *Peristedion greyae,* holotype. Ventral view of head, showing barbel arrangement.

parietal spines 10.8 (22.6). Nape length 8.2 (17.2). First (posterior) serrated ridge on mandible, length 2.8 (5.9), width 1.1 (2.3). Second (middle) serrated ridge on mandible, length 2.8 (5.9); width 0.6 (1.3). Third (anterior) serrated ridge on mandible present, minute, not measured. Fourth suborbital ridge, length 7.3 (15.3), width 0.7 (1.5). First ventral scute length 15.8 (33.1), width 9.9 (20.7). Second ventral scute length 9.7 (20.3), width 11.3 (23.6).

Specimen originally preserved in 10 per cent formalin, neutralized, and changed to 40 per cent isopropanol. Spiny dorsal fin tan with a dusky stripe near edge. Soft dorsal fin tan with a narrow dark edge. Anal fin tan. Pectoral fin pinkish tan, distal one-third black (dark red in life). Pelvic and free rays of pectoral fin yellowish tan. Caudal fin yellowish tan with a dark dorsal edge. Chin and lip barbels pinkish tan. Body yellowish tan. Dorsal portion of head pinkish brown, ventral portion pink.

Description of the Species.—Ranges of measurements from type material given in Tables 1 and 2. Counts from 60 type specimens unless otherwise denoted under section on methods.

FINRAYS: Dorsal spines 8; dorsal softrays 18 to 20 (modally 20); an-

TABLE 1

SELECTED MEASUREMENTS OF *Peristedion greyae* TYPE SPECIMENS EXPRESSED AS RANGES IN PERCENTAGE OF STANDARD LENGTH

Character	Size Range	
	60 to 97 mm (SL) (30 Paratypes)	102 to 183 mm (SL) (Holotype and 29 Paratypes)
Joined pectoral finray length	16.5-21.4	16.2-21.3
First free pectoral finray length	17.8-22.8	18.7-23.6
Second free pectoral finray length	12.6-18.7	14.0-18.2
Pelvic finray length	20.2-25.1	19.5-24.6
Head length	32.7-42.1	33.7-39.1
Greatest head width	24.9-33.9	27.2-33.9
Body depth at first dorsal spine	16.0-21.1	16.2-20.8
Body depth at anal fin origin	10.5-12.9	9.7-13.1
Body width at pectoral fin origin	12.2-16.9	14.4-20.0

terior four dorsal spines usually on first and second dorsal scutes, remaining spines one per scute; first two dorsal softrays at the scute following last dorsal spine; remaining softrays usually one ray per scute; last dorsal spine and last softray sometimes very small, scarcely visible. Anal softrays 18 to 21 (modally 20); first and last ray smaller than adjoining rays, either unsegmented or segmented only on distal half (lack of segmentation in the first anal finray has caused it to be classified as a spine; see Jordan & Evermann [1898: 2179]). Joined pectoral finrays 11 to 13 (modally 12), plus two free rays; first (dorsalmost) free ray longer than joined rays, and extending past anal origin. Pelvic finrays I-5; spine translucent, leading edge smooth; median edge of fin adnate to lateral edge of first ventral scute. Caudal finray counts 8-9+7+6+8-9 based upon 21 stained specimens.

BARBELS: Lip and chin barbels slender, less than 0.2 mm wide. Lip barbel half-counts from type specimens: 95 per cent with 4/2 lip barbels, usually grouped 2+2 barbels; 2.5 per cent with 5/2, grouped 2+3 barbels (some specimens mutilated, counts not determinable). Chin barbel half-counts from type specimens: 84 per cent with 12-13/5, usually grouped 3+3+3+2+1 or 3+3+3+2+2 (Table 3). Filamentous barbel: moderately long, usually not reaching termination of perifacial rim; terminating posteriorly in three or four filaments; filaments along barbels, arranged in clusters of two each in a row on one side and on other side a single filament opposite each pair (Fig. 5).

GILLRAKERS ON FIRST ARCH: Epibranchial gillrakers, 5 to 7, modally 6; 5 gillrakers in 70 per cent of 30 specimens from 60 to 99 mm SL, and 6 gillrakers in 73 per cent of 70 specimens of 100 to 180 mm SL; rakers graduated in length, long and slender at angle, small tubercle anteriorly.

TABLE 2

SELECTED MEASUREMENTS OF *Peristedion greyae* TYPE SPECIMENS EXPRESSED AS RANGES IN PERCENTAGE OF HEAD LENGTH

Character	Size Range 60 to 97 mm (SL) (30 Paratypes)	Size Range 102 to 183 mm (SL) (Holotype and 29 Paratypes)
Filamentous barbel length	27.2-43.9	32.1-50.1
Lip barbel length	5.1-12.2	6.5-12.4
Chin barbel length	3.2-9.8	4.1-8.6
Snout length	42.2-48.6	44.4-48.9
Least width of snout	31.9-41.2	33.3-37.4
Orbital length	21.3-30.2	22.1-27.0
Orbital depth	17.0-22.8	15.1-20.7
Interorbital width	19.9-27.0	16.5-21.8
Rostral exsertion length	24.0-35.9	21.1-37.8
Width between rostral exsertions, near base	16.8-23.8	17.8-23.2
Greatest width of rostral exsertion	12.0-15.4	11.7-13.7
Width of rostral exsertion at middle	6.0-7.8	5.1-7.4
Distance between tips of rostral exsertions	23.1-39.3	26.1-38.2
Distance between parietal spines	19.6-31.0	18.8-25.4
Nape length	16.5-22.7	14.2-19.5
First (posterior) ridge on mandible length	4.5-7.7	5.1-8.7
First (posterior) ridge on mandible width	1.2-10.2	1.3-4.2
Second ridge on mandible length	2.7-8.3	3.4-8.6
Second ridge on mandible width	0.3-2.2	0.6-3.3
Fourth suborbital ridge length	13.0-19.9	13.5-19.6
Fourth suborbital ridge width	1.2-3.5	1.1-2.5
First ventral scute length	24.6-34.4	25.2-36.1
First ventral scute width	15.5-23.9	17.4-27.0
Second ventral scute length	13.7-20.1	14.3-21.2
Second ventral scute width	14.3-21.2	17.7-29.1

Ceratobranchial gillrakers 16 to 21, modally 19, decreasing in size anteriorly, posterior 6 rakers near angle equal to or larger than gillraker at angle. Hypobranchial gillrakers, 3 to 5, modally 4; decreasing in size anteriorly to a small raker or tubercle. Gillrakers of lower limb 20 to 26, modally 23. Total gillrakers of first arch 24 to 32, modally 27.

SPINES AND RIDGES OF HEAD: Nasal, mesethmoid, lateral ethmoid, preocular, supra-ocular, and postocular spines absent. Rostral exsertion spine small, not exceeding 1.3 mm; absent in one paratype. Frontal I spine variable, a tubercle, a low retrorse spine, or an elevated spine. Frontal II spine variable, absent, a low ridge, or a small spine 0.2-2.3 mm at posterior termination of ridge. Parietal spine variable, ranging from a low retrorse spine to an elevated spine, 0.9-6.5 mm; relatively longer in relation to

TABLE 3

Chin Barbel Half-counts[1] and Number of Groups From the Type Specimens of *Peristedion greyae*

Number of barbel groups	Number of barbels							
	9	10	11	12	13	14	15	16
4	2	2	1	2	–	–	–	–
5	–	–	4	84	14	5	1	–
6	–	–	–	–	–	–	–	1

[1] Half-counts from mutilated specimens omitted.

head length in postlarvae and juveniles than in adults. Pterotic ridge low. Post-temporal ridge low, ascending posteriorly, terminating bluntly. Opercular ridge terminating in a flat spine extending beyond posterior edge of opercle; edge of ridge weakly serrated or spinous; in postlarvae and small juveniles, termination of ridge at posterior edge of opercle blunt or slightly rounded. Perifacial rim: on second infraorbital variable, absent, a spine or spines, or a ridge bearing one to six spines or large serrations; on third infraorbital, a narrow shelf anteriorly, moderately wide shelf posteriorly, often coalesced but usually distinguishable; on preopercle, delineated anteriorly by suture of preopercle with third infraorbital, increasing in width posteriorly to sensory system in rim, then decreasing in width as a strong concavity (absent in one paratype), then increasing in width, and finally terminating posteriorly as a broad shelf with posterior margin nearly perpendicular to head. Second infraorbital ridge narrow, extending posteroventrally from perifacial rim, dorsal and nearly parallel to the maxillary with mouth closed, terminating above posterior serrated ridge of mandible. Fourth infraorbital ridge narrow, width 0.4-1.2 mm, located below eye; with growth, ridge lengthens but does not widen (ridge 3.3-6.4 mm long in specimens less than 100 mm SL, 4.4-12.7 mm long in specimens greater than 100 mm SL). Preopercular dorsal ridge short, wide, not visible in dorsal view of head, located posterior to termination of ridge on second infraorbital. Preopercular anterior ventral ridge, size equal to posterior ridge of mandible, near edge of preopercle immediately posterior to first ridge of mandible; preopercular posterior ventral ridge, near or on ventral edge of preopercle, with large openings of preoperculo-mandibular canal on either side of ridge. Rostral exsertions (= first infraorbitals or lachrymals), flat, narrow, moderately long, diverging slightly with mouth closed (may be parallel or convergent with mouth open), tips rounded, lacking strong serrations.

Spines and Scutes of Body: Nuchal spine of nuchal scute ("nuchal scute" called "dorsal plate" by Teague, 1961), absent or as long as 3.6

mm; smaller than spine on first scute of dorsal series. Dorsal series, 25-27 scutes (modally 26); size of spines on scutes decreasing posteriorly; posterior two spines usually small and laterally oblique to others in series. Superomedian series, 32 to 35 scutes (modally 33); four scutes in arch at anterior end of series always bearing small ridges, whereas second to fourth scutes may bear tubercles or spines on ridges; size of spines increasing posteriorly to sixth to ninth scutes; posterior 7 to 11 scutes (modally 9), in series bear bicuspid spines; posterior two scutes on caudal base and caudal peduncle may lack spines, or may have unicuspid or bicuspid spines. Inferomedian series, 23 to 26 scutes (modally 24); normally first scute and spine at anterior end of series twice the length of the second scute and spine, with outer edge of first spine straight; posterior two or three scutes in series fused with ventral series; spines on these scutes usually aligned with the inferomedian and ventral spines. Accessory series, 0 to 3 scutes (modally 0); 1 to 3 scutes in 7 of 60 type specimens examined, beneath anterior scutes of inferomedian series. Ventral series: 22 to 24 scutes (modally 23); first ventral scute (first pair of abdominal keeled plates as defined by Teague, 1961) with spines obsolete (32 specimens), or with tubercles (19 specimens), or with spines (9 specimens); anterior edge of first ventral scute posterior to bony ridge of pelvic girdle, visible beneath skin (Fig. 3); second ventral scute (second pair of abdominal keeled plates) with spines lacking or obsolete (10 specimens), or with tubercles (39 specimens), or with spines (11 specimens); anus located between second and third scutes (52 specimens), or on third scute (3 specimens), or between third and fourth scutes (5 specimens); spines on third or fourth scute nearly equal in size with spines on succeeding scutes decreasing in size posteriorly with last scute in series bearing small spine; last distinguishable ventral scute usually at posterior anal finray or immediately posterior to last anal finray. Caudal series: number constant, two dorsal, one lateral, and two ventral scutes; anterior dorsal and ventral caudal spines small, approximately one-half the length of the posterior spines; spine on lateral caudal scute long, slender, extending past the end of posterior dorsal caudal-fin spine; edges of caudal spines usually smooth, but sometimes with small serrations. Scutes lacking in small area on side immediately posterior to base of pectoral fin.

INTERNAL ANATOMY: Intestine extending from stomach along right dorsal side to posterior edge of abdominal cavity, looping ventrally, extending backwards to anterior end of abdominal cavity on right side, angling inwardly to ventral median surface immediately posterior to stomach, and then extending posteriorly along median ventral surface of abdominal cavity to anus. Peritoneum translucent yellow, the air bladder silvery in preservative. Vertebrae 33 to 35 (modally 34). Branchiostegal bones seven.

Coloration: Variable, but generally as follows in freshly caught specimens. Spinous dorsal fin pink, with a very dark red band near or on edge. Soft dorsal fin pink, with a narrow dark red band on edge. Pectoral fin: four coloration bands across fin, a broad band of light red at base, a broad band of pink, a broad band of very dark red, and a very narrow band of pink at the margin. Caudal pink, distal portion and dorsal edge dark red. (Dark red markings on fins of fresh material appearing black in preservative.) Anal fin pinkish white. Pelvic fins and free rays of pectoral pale red. Mandibular barbels pale red. Chin and lip barbels pink or white. Body pink above superomedian series of scutes; a broad band of bronze, golden yellow, or white between superomedian and inferomedian series. Abdomen white, ventral portion of body posterior to anus pink, dorsal portion of head pink, ventral portion of head orange-pink.

Range.—The known range is from Cape Lookout, North Carolina in the western North Atlantic, southward through the Gulf of Mexico and Caribbean Sea to Tobago Island (Lesser Antilles). This species occurs at depths of 100 to 455 fathoms (183-830 m) and is common off eastern Florida in 180 to 225 fathoms (330-411 m). The largest specimen examined, 190 mm SL, was taken in the Gulf of Mexico, south of Mobile Bay, in 250 fathoms (457 m).

Common Name.—Prickly armored searobin, in reference to the sharp spines on the scutes.

Etymology.—This species is named for the late Marion Grey, Chicago Natural History Museum, in recognition of her many contributions to the knowledge of the bathypelagic and benthic fish fauna.

Material Examined.—The type series does not include all specimens examined. Some were examined only for selected and diagnostic characters. Specimens examined are listed geographically from north to south in the following manner: for type specimens examined, museum number or collection, number of specimens, range of standard length in millimeters (in parentheses), vessel and station number or location, latitude and longitude, depth in fathoms, and date of capture; for other specimens examined, the latitude and longitude, depth in fathoms, and date of capture were omitted.

Holotype: USNM 198124 (132 mm), Silver Bay sta. 3665, 29°40′N, 80°11′W, 80-foot flat trawl on bottom, 165 fms, Jan. 17, 1962.

Paratypes: SU 62138, 3(78-109), TU 33302, 2(77, 106), UMMZ 181426, 3(74-110), UMML 14796, 3(89-109), CU 47245, 3(81-105), UW 17776, 3(90-103), Silver Bay 4159, 34°15′N, 75°54′W, 190-200 fms, June 9, 1962.—TABL, 2(96-97), Silver Bay 4218, 30°05′N, 80°10′W, 170-175 fms, Aug. 23, 1962.—USNM 198125, 5(119-141), MNHN 1964-286, 1(70), LMNH 24871, 1(84), Silver Bay 3665, 29°40′N, 80°11′W, 165 fms, Jan. 17, 1962.—ANSP

101601, 1(80), MCZ 43031, 1(94), BMNH 1964.8.31.1, 1(93), Silver Bay 4223, 29°30′N, 80°08′W, 180-185 fms, Aug. 24, 1962.—TABL, 4(60-68), IRSNB I. G. 23153-No. 462, 1(77), AM IB-7246, 1(85), MN Ict. 9747, 1 (88), IM, 1(90), BOC 4493, 1(89), Silver Bay 4227, 29°20′N, 80°05′W, 183-195 fms, Aug. 24, 1962.—USNM 198126, 4(63-84), CNHM 66701, 1 (126), Combat 441, 25°16′N, 80°00′W, 185 fms, July 22, 1957.—MNHN 1964-287, 1(131), LMNH 24872, 1(136), IRSNB I. G. 23.153-No. 461, 1 (134), AM IB-7247, 1(148), MN Ict. 9746, 1(138), IM, 1(143), BOC 4494, 1(150), Oregon 3582, 9°15′N, 81°32′W, 250 fms, May 25, 1962. CNHM 66702, 1(95), ANSP 101602, 1(126), MCZ 43032, 1(135), BMNH 1964.-8.31.2, 1(140), Oregon 3598, 9°03′N, 81°22′W, 200-220 fms, May 31, 1962. —TABL, 5(126-183), Oregon 3599, 9°00′N, 81°23′W, 250 fms, May 31, 1962.

Other Specimens: All specimens not listed from other collections are deposited in the TABL (Tropical Atlantic Biological Laboratory, Miami, Florida) fish collections. Abbreviations used for exploratory fishing vessels are SB-Silver Bay, Ore-Oregon, Pel-Pelican, and Comb-Combat. Comb 172, 1(79); SB 4160, 6(102-115); SB 4161, 1(56); Comb 179, 1(176); Comb 291, 1(106); Comb 288, 1(45); Comb 295, 3(49-106); Comb 296, 1(148); Comb 300, 4(38-97); Comb 307, 1(48); Comb 310, 1(48); SB 228, 1(136); SB 4214, 2(100-134); Pel 42, TU 14762, 1(131); SB 3078, 3(130-142); Comb 499, USNM 159842, 1(132); Pel 58, USNM 156607, 1(135); Pel 57, UMML 3414, 1(148); SB 3746, 3(95-136); Comb 430, 17(120-148); SB 3739, 2(129-140); SB 3740, 8(120-140); SB 5455, 7(122-139); SB 4215, 8(120-142); SB 3080, 22(127-160); SB 3741, 4(90-130); SB 4212, 2(131-144); Comb 322, 2(136-140); SB 3752, 6(120-144); Comb 431, 3(124-132); Comb 433, 9(122-141); SB 3747, 4(128-145); SB 4213, 1(135); Pel 56, 1 (117); SB 3082, 16(104-150); SB 3675, 5(121-132); SB 3683, 40(113-147); SB 3081, 10(130-142); SB 4216, 15(125-149); SB 3085, 10(117-142); SB 3084, 7(118-138); SB 3661, 51(113-142); Pel 46, USNM 158166, 1(131); SB 4363, 1(146); Comb 323, 1(128); Comb 434, 3(119-139); Comb 313, 1 (130); SB 4219, 62(118-168); SB 3742, 5(126-140); Comb 499, USNM 159842, 1(133); Comb 473, 1(131); SB 3664, 76(110-147); Comb 435, 2 (125-126); SB 3083, 3(129-132); SB 3748, 2(129-139); SB 5456, 20(119-137); SB 4220, 37(137-162); SB 211, 1(94); Comb 324, 3(129-133); Comb 194, USNM 159841, 1(124); SB 4221, 23(137-168); Comb 314, 1(134); SB 218, 1(135); SB 4222, 23(137-168); Pel 31, USNM 158165, 1(149); SB 1607, 1(132); Comb 325, 1(124); SB 3750, 3(109-142); Pel 77, TU 16318, 2(124-140); Comb 475, 3(121-133); Comb 484, 1(130); Comb 483, USNM 159836, 1(119); Antillas, UMML 4496, 2(75-142); SB 220, 3(80-102); Comb 486, USNM 159848, 2(127-130); SB 225, 1(65); SB 2064, 2(133-136); SB 3075, 51(120-146); SB 5459, 13(127-144); SB 226, 2(95-114); SB 4224, 128(99-167 T.L.); SB 1608, 1(136); SB 2067, 2(136-142); SB 5460, 5(123-140); Comb 479, 2(123-126); SB 227, 3(96-139); Ore 599, CNHM 45641, 1(58); SB 221, 1(117); Ore 319, TU 2813, 2(157-161); SB 4227, 9(62-101); SB 4227-4228, 680(70-176); Comb 476, 4(135-143); SB 4225, 15(125-168); SB 3076, 63(117-155); Ore 1246, USNM 157857, 2(104-116); Comb 329, USNM 159849, 2(123-128); Ore 1964, CNHM, 1(133); Ore 1519, TU 11673, 2(125-133); SB 2070, 5(130-142); Ore 3652, 29(110-190); Ore 1965, CNHM, 2(164-166); Ore 1581, USNM 158160, 1(121); Ore 3653, 5(132-174); Ore 3677, 2(59-89); Ore 1963, CNHM, 3(106-185); Ore 3218, 2(155-162); Ore 279, CNHM 465582, 10(157-172), USNM 158162, 26(140-172); SB 4230, 105 discarded; SB 5476, 11(127-145); Gulf Master, UMML 4016, 6(84-133); Ore 1568, UMML 591, 2(125-150); Ore 3390, 11(132-170); SB 4231, 8 discarded; SB 4232, 600 (90-180); Ore 4005, 10(138-160); Comb 317, 1(121); Ore 4786, 1(90); Ore 1388, USNM 157859, 2(67-80); Ore 4822, 5(123-162); Albatross 2376, USNM 44673, 1(127); Ore 126, 1(143); Ore 127, USNM 158521, 2(140-163); Ore 4014, USNM, 1(96); Ore 1276, USNM 157860, 3(114-118); Comb 331, 2(131-140); Pel 29, UMML 1856, 1(123); SB 5478, 8(130-142); Comb 332, 6(83-150); SB 5479, 2(121-126); Albatross 2397, USNM 44232, 8(144-169), SU 9511, 1(156); SB 4238, 48(133-160); SB 3073, 10(124-145); Antillas, UMML 4501, 1(153); SB 4240, 300; Pel 66, TU 14818, 1(136); Comb 319, 1(134); SB 3072, 3(121-133); Ore 1276, USNM 157860, 3(113-145); SB 4241, 50(94-166); Pel 27, UMML 18, 1(117); SB 3095, 130(117-146); Pel 13, UMML 30, 8(117-136), USNM 158163, 2(128-137); SB 3711, 57(104-153); SB 4242, 22(136-163); Pel 20, UMML 19, 1(129); Pel 25, 5(50-132); SB 4245, 52(128-161); Ore 4615, 1(77); Ore 4709, 8(87-156); Ore 489, USNM, 2(147-151); Ore 4730, 1(119); Pel 10, UMML 102, 2(115-119); Ore 4611, 2(81-82); SB 3472, 2(70-95 T.L.); Gerda 175, UMML 14292, 1(142); Ore 162, USNM 185074, 1(107); Ore 163, USNM 158239, 4(56-143); Comb 460, 2(128-136); Ore 1091, TU 12911, 3(90-95); Ore 1556, TU 12671, 39(64-145); Gerda 29, UMML 15, 15(51-91); USFWS, UMML 9087, 1(128); Gerda 266, UMML 14726, 1(126); Gerda 76, UMML 11951, 1(106); Comb 442, 4(51-78); Gerda 61, UMML 14703, 1(135); Comb 453, 4(67-103); Gerda 229, UMML 13880, 1(115); Comb 438, 2(73-108); Gerda 228, UMML 14274, 3(100-122); Comb 439, 2(97-103); SB 3518, 5(62-81); Ore 1321, CNHM 64258, 4(69-99); SB 3517, 1(106); Comb 186, UMML 1852, 1(135); Ore 1010, USNM 188230, 2(122-129); Ore 1009, 5(124-141), USNM 164121, 3(134-138); Ore 1328, TU 14794, 1(76); Ore 2671, CNHM, 6(107-134); Ore 4362, UMML 13287, 1(139); Ore 1538, TU 12706, 20(53-154); Ore 1537, TU 12733, 9(105-150); Ore 1011, USNM 157821, 2(76-125), CNHM 61326, 2(52-99); Ore 4528, 4(125-136); Ore 4373, UMML, 1(133); Ore 2670, CNHM, 15(109-145); Ore 1007, USNM 164122, 11(72-156), TU 10919, 4(89-145); Ore 1548, TU 12701, 37(46-152); Ore 1016, CNHM 61329, 1(139); Ore 1005, USNM 164125, 3(50-74), TU 10906, 5(70-162); Ore 1330, USNM 157883, 4(56-119); Ore 1012, TU 11012, 3(122-150); Comb 281, UMML 2881, 1(121); Comb 436, 2(110-121); Fish Hawk 7512, USNM 142973, 1(92); SB 2458, 3(158-165); Tortugas, USNM 117050, 8(81-145); Tortugas, USNM 117051, 2(135-138); Tortugas, USNM 117052, 1(55); Tortugas, USNM 92039, 22 (84-148); Tortugas, USNM 92065, 12(100-112); Ore 726, CNHM 45638, 16(115-149); Ore 590, 1(119); Ore 1054, 1(56); Ore 3629, 1(169); Ore 3628, 2(137-150); Ore 1885, CNHM, 3(62-67); Ore 1883, CNHM, 1(56); Ore 3627, 4(118-142); Ore 3616, 3(139-141); Ore 3565, 6(124-143); Ore 3571, 2(134-140); Ore 3570, 2(135-137); Ore 3614, 1(141); Ore 1923, USNM 159844, 1(156); Ore 3575, 22(138-185); Ore 3609, 2(141-143); Ore 3576, 1(149); Ore 3610, 2(137-145); Ore 4922, 3(159-162); Ore 4407, 8 (70-183); Ore 4406, 6(133-176); Ore 4408, 3(122-135); Ore 4412, 6(158-180); Ore 4419, 2(133-156); Ore 5037, 1(116); Ore 2780, FSBC (VGS 60-76), 2(125-133); Ore 2777, 1(183); Ore 2353, 1(144); Ore 2779, 2(163); Ore 2775, 3(119-157); Ore 5029, 3(161-173); Ore 5028, 1(165); Ore 4440, 2(95-149); Ore 4842, 1(139); Ore 4841, 21(127-177); Ore 4839, 1(155); Ore 4859, 1(168); Ore 4441, 1(152); Ore 4448, 1(175); Ore 4882, 7(142-186); Ore 3584, 3(134-146); Ore 3600, 3(130-148); Ore 3592, 1(145).

Confusion of P. greyae *with* P. longispatha.—Using existing keys (Longley & Hildebrand, 1941:167-168; Teague, 1961:4-6), specimens of *P. greyae* would be identified as *P. longispatha.* Review of the literature and examination of the type series of *P. longispatha* and the holotype of *P. bartschi* explain this confusion.

In the original description of *P. longispatha*, Goode & Bean (1886: 166-167) designated the type as being from BLAKE LVIII, in 314 fathoms (575 m) off Santa Cruz, and the remaining type series from BLAKE LXII and LXIII, and ALBATROSS sta. 2358, 2376, 2397, and 2407. The single specimen from BLAKE LVIII is the holotype, and the remaining specimens listed are paratypes. Subsequently, Goode & Bean (1896:472) omitted ALBATROSS sta. 2407 from the list of the type series, as this station had been erroneously included, and they also changed the depth and locality of the holotype to 242 fathoms (443 m) off Havana. They apparently were unaware that the Roman numerals on specimen labels were sorting numbers, and not station numbers (Eschmeyer, 1965:236-238). When Goode & Bean discovered that the collection data with the Roman numerals were different from the data with the Arabic numerals, they incorrectly changed the locality data to agree with that given for the Arabic numerals. The correct data for the holotype of *P. longispatha* (MCZ 28009) are BLAKE sta. 129, sorting number LVIII, 17°42′35″N, 64°54′20″W, in 314 fathoms (575 m), bottom water temperature 48.5°F (9.2°C), off Frederickstadt (= Frederiksted), Santa Cruz (= St. Croix), on January 4, 1878.

The holotype and four other specimens of *P. longispatha* from the BLAKE stations in the Museum of Comparative Zoology were cataloged as syntypes. Two of these four specimens are not paratypes, as they are from stations not included in the type series: MCZ 28088, BLAKE sta. 275, 12°58′33″N, 59°36′45″W, in 218 fathoms (399 m) off Barbados, and MCZ 28090, BLAKE sta. 172, 15°58′10″N, 61°42′55″W, in 62 fathoms (113 m) off Guadeloupe. The remaining two specimens, MCZ 28022, Sorting No. LXII and MCZ 28089, Sorting No. LXIII, both from BLAKE sta. 274, 13°00′50″N, 59°36′20″W, in 209 fathoms (382 m) off Barbados, are paratypes. None of these four is *P. longispatha*; MCZ 28088, 28089, and 28090 are *P. antillarum* Teague 1961; and MCZ 28022 is *P. imberbe* (Poey, 1861). I have redescribed and discussed *P. imberbe* in a manuscript now in preparation on those peristediids having a narrow perifacial rim.

Teague (1961:12) did not discuss the type specimens listed by Goode & Bean from the ALBATROSS stations in his description of *P. longispatha,* nor did I find a record of these types in the Museum of Comparative Zoology. However, in my examination of peristediids in the U. S. National Museum, I found the following type specimens of *P. longispatha* entered in the general collections: USNM 47648 (1), BLAKE sta. 274, Sorting No. LXIII, in 209 fathoms off Barbados, which I reidentified as *P. antillarum*; USNM 44673 (1), from ALBATROSS sta. 2376 and USNM 44232 (8), from ALBATROSS sta. 2397, reidentified as *P. greyae*; and USNM 46031 (1), ALBATROSS sta. 2358, originally identified and cataloged as *P. longispatha,* changed to *P. caribbaeum* Myers (MS), later identified as *P. bartschi* Myers, which I identified as *P. longispatha.* The only specimen of *P. longispatha* designated as a paratype is USNM 46031 from ALBATROSS sta. 2358.

Dr. Walter Courtenay, Jr. (personal communication) stated that a specimen removed from USNM 44232, ALBATROSS sta. 2397 in 1892, was given to the Stanford University collections. This specimen, SU 9511, is in the general collections and was not listed by Böhlke (1953) in the type material of Stanford. The specimen is *P. greyae*, as are others in the USNM collections from this station.

Teague's (1961:13-14) description of *P. longispatha* is a composite of three species. In addition to the holotype of *P. longispatha*, he used specimens of *P. imberbe* (MCZ 28022) and *P. greyae* (USNM 117051 and USNM 210952).

In his discussion of *P. bartschi*, Teague (1961:13) seriously questioned whether rostral exsertion and nasal spines are present in juveniles (USNM 46031) and are vestigial or obsolete in the adults (USNM 93186 and USNM 158161). I identify his specimens labelled *P. bartschi* as *P. longispatha.* Ontogenetic changes in rostral exsertion and nasal spines are found not only in *P. longispatha* but also in *P. schmitti.* The changes in spination apparently confused Teague (1961:5, 17), for in his key to the peristediid species he separated *P. schmitti* from *P. altipinnis* Regan, 1903, by the presence of rostral exsertion and nasal spines on *P. schmitti*, whereas in his type description of *P. schmitti* he listed the rostral exsertion spines as usually absent or vestigial, and the nasal spines as usually absent. The validity of the species in the *P. roseum* Miranda-Ribeiro, 1903—*P. altipinnis-P. schmitti* group remains to be resolved.

Myers (1934:10-12, Fig. 2) described *P. bartschi* apparently without comparing his holotype to the holotype of *P. longispatha.* In dorsal view, the head of the holotype of *P. longispatha* (Fig. 7), does not differ from that of *P. bartschi* in the characters used by Myers to separate the two species. I speculate that Myers compared his holotype with specimens of *P. greyae* which were incorrectly identified as *P. longispatha*, because *P. greyae* differs from *P. bartschi* in the same ways that Myers says *P. longispatha* differs from *P. bartschi.* I consider *P. bartschi* to be a junior synonym of *P. longispatha.*

Peristediids commonly collected off southern Florida and reported as *P. longispatha* by Longley & Hildebrand (1941:169) are probably all *P.*

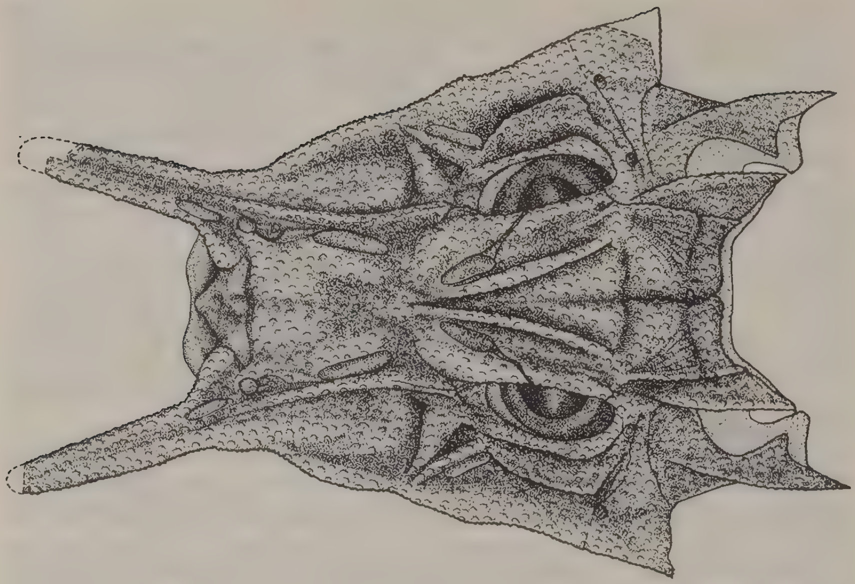

FIGURE 7. *Peristedion longispatha*, holotype, MCZ 28009. Dorsal view of head.

greyae. This premise is based on the following: (1) Longley & Hildebrand were aware of the good description and illustration of *P. bartschi* by Myers, and they would have identified similar specimens as this species; (2) specimens collected by Longley and identified as *P. longispatha* were deposited in the U. S. National Museum (USNM 92039, 92065, 117050, 117051, and 117052) and the British Museum (Natural History) (BMNH 1933.10.12.101-104), but only USNM 117052 was labeled as identified by Longley (all have been reidentified as *P. greyae*); and (3) observations on and description of *P. longispatha* by Hildebrand in Longley & Hildebrand (1941:169) were those of *P. greyae*. *P. longispatha* differs from Hildebrand's description in that it has not been commonly collected (fewer than 100 specimens are known in five major collections in the United States) and is known primarily from the Caribbean; the tip of the pectoral fin and its free rays do not reach the anal origin; it has a reticulated color pattern on the body and a dusky or black pectoral fin; and it has shorter, broader, diverging rostral exsertions. The peristediid identified as *P. longispatha* by Longley, upon which Chan (1941) based a histological study of the alimentary tract, was probably *P. greyae*.

Springer & Bullis (1956:91) reported that *P. longispatha* was taken at 21 OREGON stations in the Gulf of Mexico. I have examined material identified as *P. longispatha* from over half of these 21 stations, deposited in various museums; all are *P. greyae*; and I speculate that most, if not all, of the peristediids reported as *P. longispatha* by Springer & Bullis are *P. greyae*.

In summary, the type series of *P. longispatha* consists of 15 specimens of four species from five stations, *P. longispatha* (2 specimens), *P. antillarum* (2 specimens), *P. greyae* (10 specimens), and *P. imberbe* (1 specimen). *P. bartschi* is conspecific with *P. longispatha*. Specimens which I examined that were deposited in museums by Longley & Hildebrand and identified as *P. longispatha* are *P. greyae*. The occurrence of *P. longispatha* in the Gulf of Mexico in the species station list by Springer & Bullis (1956: 91) is probably incorrect, as specimens I examined from over half of the stations involved are *P. greyae*.

Relationships.—The three closely related species (based on anatomy) most likely to be confused with *P. greyae* are *P. truncatum* (Günther, 1880), *P. longispatha*, and *P. antillarum*. They may be readily distinguished from *P. greyae* as follows: *P. truncatum*, by the greater number of chin barbels, single, serrated ridge on the mandible, and strongly serrated opercular ridge; *P. longispatha*, by the wide head and rostrum, strongly diverging rostral exsertions, fewer lip barbels, and a shorter pectoral fin; and *P. antillarum*, by the narrow head, extremely long, slender rostral exsertions, and fewer lip and chin barbels.

The holotype of *P. spiniger* Longley & Hildebrand (1940) was examined and its anatomy is extremely similar to the illustrations of the holotype of *P. truncatum*. Teague (1961:5) was able to separate *P. truncatum* from *P. spiniger* only by the small difference in the number of chin barbels and the presence of accessory scutes beneath the inferomedian series in *P. spiniger*. I consider *P. spiniger* to be a junior synonym of *P. truncatum*, as the barbel counts given by Teague for *P. spiniger* fall within the range for *P. truncatum*, and the number of accessory scutes in *P. truncatum* examined varied from 0 to 3.

Peristedion ecuadorensis described by Teague (1961:10-11, Pl. 1) was inappropriately named, as it does not occur in the eastern Pacific, but is relatively common in the western Atlantic. When the specimens of the type series were originally cataloged in the U. S. National Museum collections, the locality data were incorrectly recorded for the ALBATROSS hydrographic sta. 2624 (from the Pacific) rather than from the ALBATROSS dredge-trawl sta. 2624 (Atlantic). The correct data for the type series of *P. ecuadorensis* are ALBATROSS dredge-trawl sta. 2624, 32°36′N, 77°29′15″W, in 258 fathoms (472 m), off Charleston, South Carolina, on October 21, 1885.

SUMARIO

NUEVA ESPECIE DE LA FAMILIA PERISTEDIIDAE EN EL ATLÁNTICO OCCIDENTAL, *Peristedion greyae*

Ejemplares del Atlántico Occidental, que habían sido identificados en el pasado como *Peristedion longispatha*, son diagnosticados como una nueva especie. Se discuten las razones por las que ejemplares de *P. greyae* han sido identificados como *P. longispatha*. Los cambios taxonómicos hechos son: *Acanthostedion* es congenérico con *Satyrichthys*; *Peristedion spiniger* es conespecífico con *P. truncatum, P. bartschi* con *P. longispatha*, *P. taeniopterum* con *P. gracile, P. mcgintyi* con *P. miniatum* y *P. schmitti* con *P. thompsoni*. Se propone el nombre "acanthostedion" para describir los estados postlarvales de los peristedios. La localidad tipo de *P. ecuadorensis* para el Océano Pacífico es incorrecta, la especie en el presente es únicamente conocida en el Atlántico Occidental.

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Food of the Threadfin Shad, *Dorosoma petenense*, in Lake Chicot, Arkansas[1]

Robert Victor Miller[2]

ABSTRACT

Forty-nine threadfin shad (36–119 mm SL) were collected in Lake Chicot, Arkansas, from 27 February to 7 November 1959. They appeared to feed on any available organism of suitable size. Organisms eaten represented more than 60 genera. Animal and plant foods were present in approximately equal amounts; protozoans and invertebrate eggs composed most of the animal food, and green algae (Chlorophyta) most of the plant food. Individual threadfin shad within a sample ate the same kinds of organisms in similar proportions. Correlations between ingested organisms and those in the plankton were significant, indicating a lack of food selectivity. There was no apparent difference in the food of fish of different sizes.

INTRODUCTION

In recent years the threadfin shad, *Dorosoma petenense* (Günther), has stimulated the interest of fishery biologists because of its value as a forage species. Threadfin shad move in large schools, feed on plankton, and are easily caught by predators. They reach a maximum length of about 9 inches, which is within the forage size of predator species such as largemouth bass. The threadfin shad is known to occur, either natively or by introduction, in lakes and rivers in West Virginia (Schwartz, 1958), Florida, Tennessee, Kentucky, Virginia, Alabama, Mississippi, Louisiana, Texas, Oklahoma, Arkansas, and California (Isaacson, 1965). The food of threadfin shad in Lake Chicot was studied because the lake was to be the source of stock for introductions of the species into new environments in Arkansas. The main objectives of the study were to identify the kinds of food organisms eaten and to determine if food selectivity was practiced.

MATERIALS AND METHODS

Forty-nine shad, 36–119 mm SL, were examined from eight collections made in 1959, from 27 February to 7 November. The collections were made with a 10-, 20-, or 40-foot seine in a small embayment of Lake Chicot, about 1.5 m deep. Immediately after capture, the fish were pithed to prevent regurgitation, and frozen on dry ice to preserve color characteristics of certain plankters.

Plankton was sampled at the time of each collection with a 10-liter, Juday plankton trap (bucket and net of No. 25 silk bolting cloth). One plankton sample was taken at mid-depth in the collecting area. Samples in the deeper, open water (6–8 m) were taken at the surface and at 1-meter depth intervals to the bottom. No major differences were found in the species and abundance of plankters in samples collected in deep and shallow water.

Organisms were identified to genus, if feasible. Identifications of invertebrates were based on Pennak (1953), and phytoplankters on Prescott (1954) and Ward and Whipple (1959). Plankton analyses using subsamples conformed to the standard methods of Welch (1948). The results for separate subsamples were averaged to determine rankings of the organisms.

After the fish were measured, weighed, and sexed, the two sections of the foregut (the pharyngeal organs and the stomach-esophagus) were removed. The contents of the pharyngeal organs were flushed into a Sedgwick-Rafter cell, and were examined as described by Miller (1964). The contents of the stomach-esophagus were subsampled because the large number of organisms present made total counts impractical. Estimates based on subsamples were compared with total counts of the various kinds of organisms for five fish caught on 7 July and two caught on 19 August. Rank correlations of the samples (0.936 and 0.983), calculated according to Snedecor (1956), were significant at the 1% level.

A modified "point system" was used to

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[1] Part of a thesis submitted to the Faculty of the Zoology Department of the University of Arkansas in 1960, in partial fulfillment of the requirements for the degree of Master of Science.

[2] Contribution No. 39, Tropical Atlantic Biological Laboratory, U. S. Bureau of Commercial Fisheries, Miami, Florida.

TABLE 1.—*Stomach contents of 49 threadfin shad collected from Lake Chicot, Arkansas, in 1959*

Ingested organisms	Frequency of occurrence (%)	Date of collection, and number of organisms									Estimated contribution to food volume[1]		
		Feb. 27	Apr. 1	May 29	Jul. 7	Jul. 30	Aug. 19	Sep. 28	Nov. 7	Total	Volume factor (Avg.)	Relative unit contribution	Percentage of total
Rotatoria	100	60	800	3,080	157	143	97	416	7	4,760	3.4	16,100	3.6
Cladocera	61	196	364	28	0	2	1	5	0	956	14.0	8,340	1.9
Copepoda	82	60	56	48	14	9	3	253	0	435	13.7	5,960	1.3
Insecta	12	1	0	1	1	1	0	8	0	12	41.6	500	0.1
Ostracoda	27	6	1	5	0	2	0	26	0	40	15.0	600	0.1
Hydracarina	4	0	0	2	0	0	0	0	0	2	20.0	40	–
Protozoa	94	156	6,084	188	9,595	30,856	79,236	42,707	37	168,859	0.9	151,970	33.6
Eggs of invertebrates	96	79	522	1,069	752	11,800	612	1,160	5	15,999	1.5	24,000	5.3
Chlorophyta	98	922	105,559	2,521	25,537	123,336	435,908	69,162	330	764,377	0.3	229,310	50.6
Pyrrhophyta	35	40	67	1	0	10	0	0	0	118	1.2	142	–
Chrysophyta	92	69	1,702	311	316	13,216	709	798	84	17,115	0.5	8,550	1.9
Cyanophyta	60	6	99	14,036	242	44	180	100	0	14,707	0.5	7,350	1.6
												452,862	100.0
Number of fish	49	9	12	12	5	3	3	4	1				
Standard length (mm)		41–84	43–71	48–77	39–67	54–104	36–65	53–119	88				
Weight (gms)		1.3–9.6	0.5–5.7	1.6–6.9	0.6–5.3	3.3–19.6	0.6–4.8	2.6–27.0	10.2				

[1] See text for details of procedure.

designate the volume of organisms. A volumetric factor was assigned to the largest organism, based on its length, width, and depth, and decreasing factors were assigned to smaller organisms. The total number of a given group was multiplied by its assigned factor to obtain an estimate of the contribution of the group to the total food ingested. Colonial forms, such as *Eudorina, Pandorina, Platydorina, Pediastrum,* and *Hydrodictyon* (all Chlorophyta), and *Anabaena* (Cyanophyta) were assigned factors based on the size of their individual cells.

Kendall's coefficient of concordance (Siegel, 1956) was used to compare the relative abundance of organisms in the stomachs of individual specimens from the May collection. The probability of the observed agreement between the stomach contents of the 12 specimens occurring by chance alone, was less than 0.01. These results permitted conclusions on food habits to be based on a limited number of specimens, and all specimens in a sample were subsequently lumped, in computing rank correlations. The similarity of the stomach contents of individuals probably was a result of the schooling behavior of the species.

FOOD COMPOSITION

The primary constituents of the diet of threadfin shad in Lake Chicot were algae (54.1%), and animal material (45.9%). Threadfin shad fed upon Diptera larvae (*Chaoborus* and tendipedids), Hydracarina, adult insects, and every major group of plankton. Over 60 genera were identified. Filamentous algae were found, predominantly as 1- or 2-cell segments. Another important group included eggs of rotifers, cladocerans, and other invertebrates. The length and weight ranges of 49 threadfin shad, the various groups of food organisms found, their frequency of occurrence, number per sample, volumetric factor, and the subsequent expansion to illustrate the relative contribution of the various organisms to the total food volume are listed in Table 1.

There were no qualitative differences between food eaten by young-of-year and yearlings (the only age groups represented). In almost all specimens, the same organisms were present in both regions of the foregut, although quantities of the various forms were less in the pharyngeal organs. For most genera (or groups) the ratio of the numbers of organisms in the stomach-esophagus to numbers in the pharyngeal organs was similar (from 3 to 4). For the rotifers, the ratio varied significantly (as shown by a chi-square test) between genera. *Conochilus, Polyarthra,* and *Trichocerca* were most abundant in the pharyngeal organs, *Brachionus* was present in essentially equal numbers in the two foregut segments, and *Keratella* and *Monostyla* were most numerous in the stomach. Miller (1964) suggested that forms predominant in the stomach may have been less digestible and may have accumulated there, whereas those predominant in the pharyngeal organs probably were digested quickly upon reaching the stomach.

Based on frequency of occurrence, the important food groups were several genera of Chlorophyta and Chrysophyta, rotifers, protozoa, cladocerans (e.g., *Bosmina, Cyclops*), and copepod nauplii.

Volumetric contributions of *Pandorina,* eggs, and filamentous algae cells were similar. The eggs and algae contributed substantially to most samples collected throughout the period, whereas 85% of the total number of *Pandorina* occurred in the August sample. Insects (including larvae) and ostracods were present in small numbers. These were consumed by a relatively small number of fish and contributed greatly to the food volume, when present. Rotifers, crustaceans, and *Eudorina* were sufficiently common to indicate that they were a steady source of food to shad.

SELECTIVITY

Selectivity of specific forms of plankton by fishes is considerably more difficult to establish than determination of qualitative feeding habits. Plankton-feeding, pelagic fishes, such as the threadfin shad, may feed in several localities or on isolated swarms of plankton. In several samples of plankton and threadfin shad, many genera of the forage organisms were present in either the foregut of the shad or the plankton, but not in both. These forms, found in small quantities (1 or 2 individuals), could have been missed in the shallow-water plankton samples, or they could have been eaten by the shad in another locality but not digested when the fish were collected.

TABLE 2.—*Rank correlations of the occurrence of food organisms in plankton samples and in contents of foreguts of threadfin shad*

Sample date 1959	Foregut and plankton	Foregut only	Plankton only	Coefficient of correlation (R's)
27 February	8	30	3	–0.40
1 April	18	17	5	0.46*
29 May	23	13	5	0.67**
7 July	17	17	6	0.78**
30 July	21	16	4	0.86**
19 August	19	15	6	0.70**
28 September	25	13	10	0.82**
7 November	12	12	12	0.81**

* Significant at the 5% level.
** Significant at the 1% level.

Rank correlations were computed for each sample in this study to compare the abundance of the various forms in the foregut of the shad with their abundance in the plankton (Table 2). In six of the eight samples, the correlation was significant at the 1% level, indicating that threadfin shad are primarily nonselective plankton feeders.

Many of the planktonic forms present in the foreguts were small enough to pass through the gill rakers, indicating that clumping of organisms or blocking of raker spaces must occur. Some bottom feeding is indicated by the occasional presence of *Chaoborus* and tendipedid larvae and unusual amounts of sand and mud. Occasional sight feeding is suggested by the presence of adult insects and mites, which probably would not have been taken if the shad fed solely by non-directed filtering of water.

DISCUSSION

Kimsey *et al.* (1957) reported that the majority of the food of threadfin shad from Lake Havasu (an impoundment on the California-Arizona border) was micro-crustacea (100% frequency of occurrence, 52% by volume). They also found that algae, present in 97% of the stomachs (40% by volume), was a major part of the diet. Kimsey (1958) determined that the principal food of threadfin shad from the Salton Sea consisted of eggs and fry of the gulf croaker (*Bairdiella icistius*), micro-crustacea, and phytoplankton, in that order.

Haskell (1959) reported that diatoms, unicellular green algae, rotifers, and crustaceans, were the principal constituents of the diets of threadfin shad he examined. He maintained that shad feed both pelagically and off the bottom by filtering water through their numerous gill rakers. These conclusions are supported by the present study.

Kimsey (1958) used the forage ratio (the "ratio of the percentage a group of organisms makes up of the total stomach contents to the percentage this group makes up of the total population of food organisms in the fish's environment") to determine that threadfin shad selected the eggs and fry of *Bairdiella* in the Salton Sea. In this study, rank correlations of foregut contents and plankton showed that threadfin shad in Lake Chicot were nonselective in their feeding. Other species of plankton-feeding, pelagic fishes have been shown to be nonselective feeders. Kutkuhn (1958) plotted regression analyses of the quantities of major taxa present in the plankton against the quantities ingested by gizzard shad (*Dorosoma cepedianum*) and concluded that, essentially, they consumed a given organism in proportion to its abundance. As the proportion of a particular organism increased in the environment, consumption by gizzard shad also increased. Using rank correlations, Hand and Berner (1959) found agreement between the occurrence of organisms in the plankton and those in the stomachs of the Pacific sardine, *Sardinops caerulea*.

Although there are several advantages of threadfin shad as a forage species (e.g., relative small size of adults, silvery color, and high reproductive potential), proposed introductions into new environments must consider the temperature range of the new body of water and the type and availability of food. Mortalities of shad have occurred in several areas when the temperature of the water dropped below approximately 45 and 54 F (Parsons and Kimsey, 1954; Hubbs, 1951). Threadfin shad are flexible in their feeding habits and probably adapt to available food supplies. Attempts at establishment of this species, therefore, should be limited to bodies of water with the required temperature range and with moderate amounts of plankton, bottom organisms, small insects, or other easily-ingested organisms.

ACKNOWLEDGMENTS

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Natural and Altered Estuarine Habitats of Penaeid Shrimp[1]

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Abstract

This study demonstrates what can happen to a shrimp nursery area when it is altered by bulkheading. Two areas were chosen — one adjacent to an unaltered vegetative shore and the other near a concrete bulkhead. Both had similar hydrology and sediment types, but differed in the amount of organic detritus in the bottom sediments and in water depth. Intensive sampling over a 10-month period produced 2.5 times more brown shrimp *(Penaeus aztecus)* and fourteen times more than white shrimp *(P. setiferus)* from the natural habitat than the bulkheaded area. This preference for the unaltered habitat depended on the physical rather than the hydrologic characteristics of the habitat.

INTRODUCTION

THE NATURAL HABITATS of the borders of estuaries of the Gulf coast are being altered or destroyed by man. Bulkheading is a common mode of alteration in Galveston Bay, Texas. This study was initiated to determine the effects on populations of postlarval and juvenile brown and white shrimp *(Penaeus aztecus* and *P. setiferus)* of bulkheading natural vegetated shore zones. Some physical and hydrographic measurements were carried out concurrently with the biological sampling to learn what differences in shrimp abundance might be associated with differences in specific estuarine characteristics. The areas chosen for study were in Clear Lake, a small body of water forming a portion of the Galveston Bay system.

DESCRIPTION OF AREA

Clear Lake is a small, protected, brackish-water estuary connected to upper Galveston Bay (Fig. 1). It is about 2.5 miles long, less than 1 mile wide and has a surface area of about 1,000 acres. Average depth is 3-4 feet, excluding a channel dredged to a depth of 6 feet. The channel extends the entire length of Clear Lake and joins a natural channel which links the estuary with upper Galveston Bay. Clear Creek, which discharges into the western end of Clear Lake, provides most of the fresh water although some enters from Mud and Taylor Lakes (Fig. 1). Sediments throughout Clear Lake are fairly uniform and vary mostly in the amount of sand present.

According to the classification scheme of Shepard and Moore (1955), sediments are predominantly silty clays in the center of the estuary, and grade into a mixed zone of sand-silt-clay along the shore.

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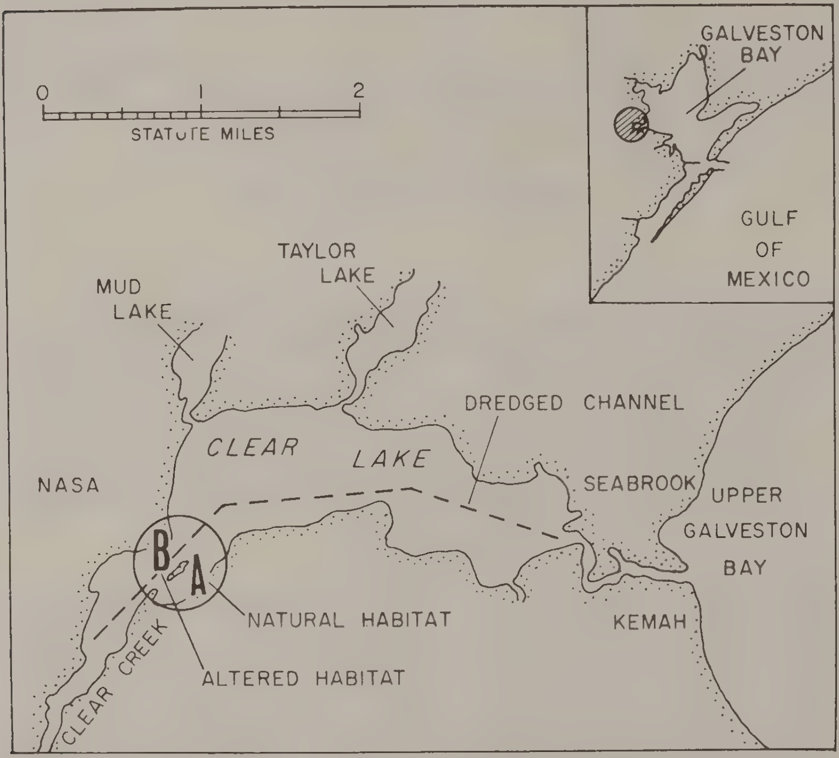
[1] Contribution No. 223, Bureau of Commercial Fisheries Biological, Galveston, Texas.

This pattern is complicated because the sources of material, topography, water circulation, and modifications by man have altered the arrangement.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1
2
STATUTE MILES
GALVESTON BAY
GULF OF MEXICO
TAYLOR LAKE
MUD LAKE
DREDGED CHANNEL
CLEAR LAKE
NASA
SEABROOK
UPPER GALVESTON BAY
B
A
NATURAL HABITAT
KEMAH
CLEAR CREEK
ALTERED HABITAT

Fig. 1. Map of Clear Lake, Texas, and vicinity.

Two areas were selected in Clear Lake for comparison (Fig. 1). Area A, a typical, vegetated shoreline, still in its natural development, represents the unaltered habitat. Area B was altered by a concrete bulkhead in 1958 (Fig. 2). Even though the two areas are about 1/3 mile apart and opposite each other, their hydrology was nearly identical.

In Area A, a vegetated zone about 120 feet wide extends from the base of a 15-foot bank to the water's edge. Two tidal zones, an upper and lower slope, were distinguished by the height of the tide and vegetation present (Fig. 3).

The shoreline of B (Fig. 3) consists of a concrete bulkhead about 1,000 feet long and 4 feet high with a 1:4-foot slope. The area directly behind the bulkhead, once a vegetated shoreline, was filled with sediments dredged from the lake side of the bulkhead. Private homes and Bermuda-grass lawns now cover the area; no natural vegetation is present. Differences in water depths between the two areas are attributed to the bulkhead at B and to dredging in the adjacent bay area (Fig. 3).

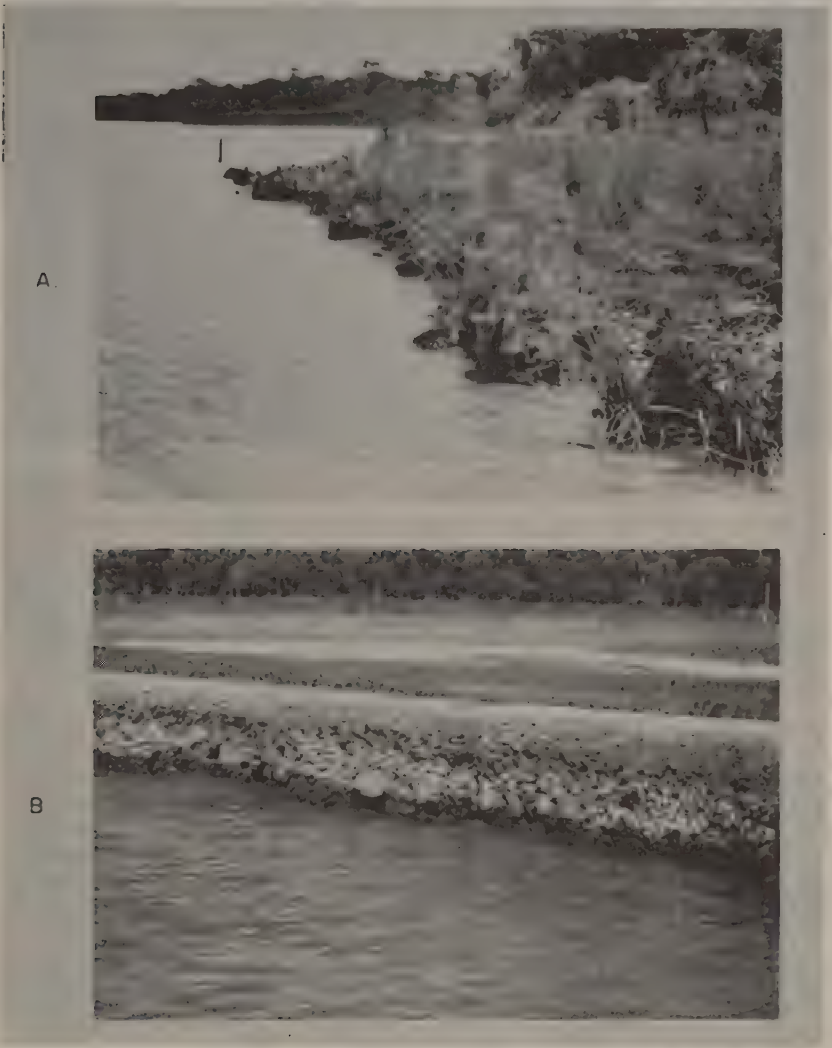

Fig. 2. Study areas. A = Unaltered Area; B = Altered Area.

METHODS

Twenty biological samples were obtained at irregular intervals between March 4 and December 8, 1965.

Personnel of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas, developed a new type of shrimp collecting gear

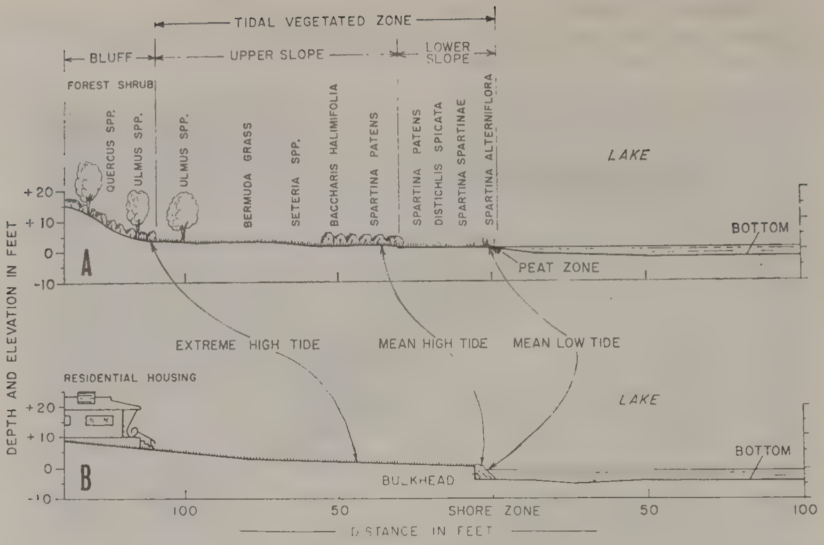
TIDAL VEGETATED ZONE
BLUFF
UPPER SLOPE
LOWER SLOPE
FOREST SHRUB
QUERCUS SPP.
ULMUS SPP.
ULMUS SPP.
BERMUDA GRASS
SETERIA SPP.
BACCHARIS HALIMIFOLIA
SPARTINA PATENS
SPARTINA PATENS
DISTICHLIS SPICATA
SPARTINA SPARTINAE
SPARTINA ALTERNIFLORA
LAKE
+20
+10
0
-10
A
BOTTOM
PEAT ZONE
DEPTH AND ELEVATION IN FEET
EXTREME HIGH TIDE
MEAN HIGH TIDE
MEAN LOW TIDE
RESIDENTIAL HOUSING
LAKE
+20
+10
0
-10
B
BOTTOM
BULKHEAD
100
50
SHORE ZONE
50
100
DISTANCE IN FEET

Fig. 3. Diagrammatic profile sketch of unaltered area A and altered area B.

(unpublished manuscript[2]) to obtain comparable samples from a variety of bottom types, including those which occur in areas A and B. A 93-foot line connected to a 7-foot bridle was attached to the front of this "marsh net." Dragging distance, therefore, was 100 feet and the area sampled was 176 square feet (16.3 square meters).

Three zones, one along the shore and the other two 50 and 100 feet from shore, respectively, were sampled parallel to the shoreline in each area. A 100-foot polyethylene line, marked at 50-foot intervals with corks, was positioned perpendicular to the shore; one end was anchored at the waterline and the offshore end was held in position by a weight placed on the bottom. After the transect line was set, the marsh net was lowered from the bow of the skiff to the lake bottom at the 100-foot cork. The skiff was then backed parallel to the shore until the 100-foot retrieving line was played out. The net was then pulled back to the skiff by hand. This method was repeated at 50 feet from shore and at the shore in each area, except along the shoreline of area A. There, the procedure was performed afoot (Fig. 4). Samples were preserved in 10% buffered (borax) formalin and lake water.

Biological samples were sorted in the laboratory, and brown and white shrimp were identified from the descriptive characteristics given by Pearson (1939) and Williams (1953). The shrimp then were divided into postlarval and juvenile groups on the basis of their total length

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[2] "A net for sampling the intertidal zone of an estuary" by Edward J. Pullen, Cornelius R. Mock, and Robert D. Ringo, Bureau of Commercial Fisheries Biological Laboratory. Galveston, Texas. 6 Ms. pp., 2 figs.

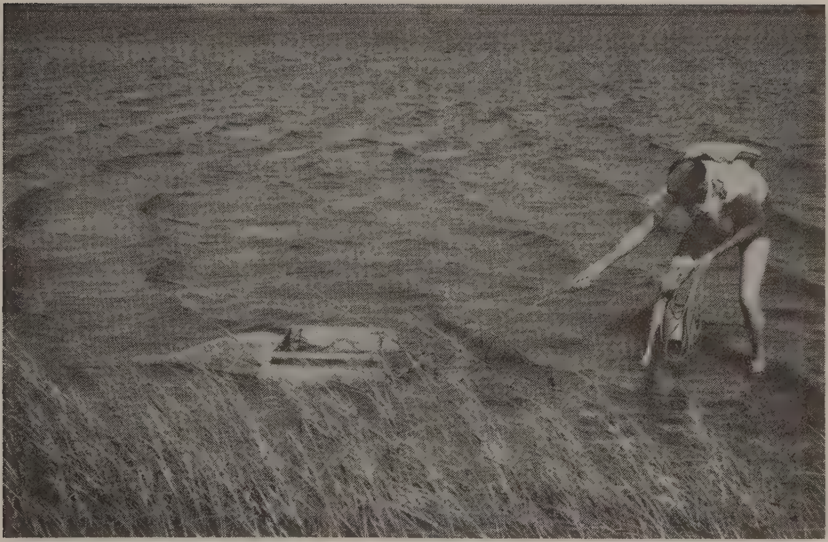

Fig. 4. Operation of the marsh net along the shore.

(from tip of rostrum to tip of telson) according to Renfro (1963). Shrimp 5 mm to 24.9 mm long were classified as postlarvae and those 25 mm to 89.9 mm long as juveniles.

Bottom water samples were collected with a Kemmerer sampler and salinities were determined in parts per thousand (ppt) (Marvin, Zein-Eldin, May, and Lansford, 1960). Bottom temperatures were measured *in situ* with a portable telethermometer and read to the nearest degree centigrade. Tidal stage and water elevation were noted visually during each collection.

On three occasions, sets of duplicate substrate samples were taken with an Eckman dredge at 5- and 10-foot intervals along each transect. Only ½ inch of sediment was removed from the dredge to sample the surface material of the bottom. These samples were analyzed for proportions of sand, silt, clay, and total organics. Sand was separated by means of standard sieves; silt and clay were identified with a soil hydrometer according to procedures employed by the U.S. Army Corps of Engineers.[3] Total organic content was determined by ignition of dried sediment samples at 1150F for 2 hours. Major types of vegetation were identified and a visual estimate made of their relative abundance.

PHYSICAL AND HYDROGRAPHIC CHARACTERISTICS

Bottom sediment along the shoreline zone at A contained a higher percentage of organic detritus than elsewhere (Fig. 5, Table 1). To pinpoint the extent of the organic material numerous samples were taken along the measured transect line in each area. The organic mat, or peat bed, extended only 2 feet from the edge of vegetation toward the open water of the system. Examination of sedimentary facies from this zone revealed that the organic material always constituted more than 40% of the sample. Farther from shore, organics represented not more than 6% of the total sample. Corresponding samples tested from B never exceeded 6% organic matter, even along the shore.

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[3] From unpublished report, Galveston District Soils Laboratory, Fort Point, Galveston, Texas.

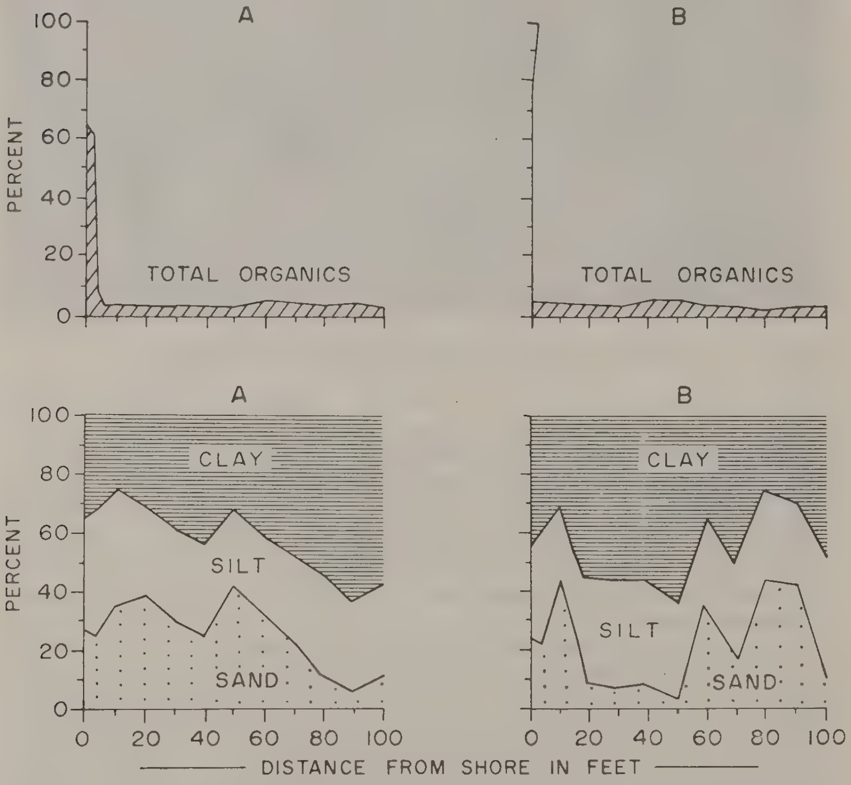

Fig. 5. Percentages of sand, silt, clay, and total organics along transect lines for the unaltered area A and the altered area B.

Sediment characteristics along the 100-foot transect at A consist of a rather uniform mixture classified as sand-silt-clay after Shepard and Moore (1955). Between 50 feet and 100 feet from shore, the amount of clay increases and sand decreases so that beyond 80 feet the sediments are silty clay. The amount of silt was almost constant throughout the transect, ranging from 25% to 43%. This orderly arrangement and progression of sediments was not present along the transect at B. Instead, sediments varied alternately between sand-silt-clay and silty clay.

TABLE 1a

PERCENTAGES OF SAND-SILT-CLAY AND TOTAL ORGANICS IN RELATION TO DISTANCE FROM SHORE FOR EACH AREA

Station and distance from shore (feet)	Water depth (inches) MLT[1]	Percent sand		Percent silt		Percent clay		Percent organics	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Unaltered Area A									
Shore	4	26	22-39	39	20-42	35	30-41	63	42-84
1	4							58[2]	
2	5							60[2]	
3	7							3[2]	
4	10							3[2]	
5	11	25	20-30	43	41-47	32	29-34	3	2- 5
10	15	35	20-43	40	30-52	25	22-27	3	1- 5
15	20	37	32-44	35	26-44	28	25-30	4	2- 6
20	21	38	35-44	32	25-38	30	25-31	5	4- 6
30	21	29	25-33	32	26-38	39	35-41	4	4- 4
40	23	25	21-30	31	24-40	44	44-45	4	3- 4
50	23	42	40-46	26	20-31	32	30-34	3	1- 5
60	25	33	20-37	25	20-36	42	38-44	6	5- 6
70	25	23	20-30	30	28-33	47	37-52	5	5- 5
80	24	12	10-13	35	30-41	53	50-57	4	3- 5
90	26	6	4-10	30	28-34	64	62-68	5	4- 6
100	26	11	7-15	31	24-37	58	50-61	3	1- 5

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[1] MLT—mean low tide.

[2] One set of samples.

TABLE 1b.

PERCENTAGES OF SAND-SILT-CLAY AND TOTAL ORGANICS IN RELATION TO DISTANCE FROM SHORE FOR EACH AREA

Station and distance from shore (feet)	Water depth (inches) MLT[1]	Percent sand		Percent silt		Percent clay		Percent organics	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
Altered Area B									
Shore	36	23	20-23	32	30-32	45	43-47	5	5- 6
5	36	21	20-23	37	21-42	42	30-56	5	5- 6
10	39	45	42-50	25	20-29	30	30-32	5	5- 5
15	39	23	20-29	32	23-38	45	43-48	5	5- 5
20	39	10	8-15	34	27-41	56	55-58	4	5- 6
30	39	9	7-13	34	29-39	57	55-58	3	3- 4
40	37	10	10-11	33	33-34	57	56-57	6	5- 6
50	35	5	3- 7	31	28-35	64	60-65	6	5- 6
60	34	36	20-40	29	20-38	35	20-50	4	3- 5
70	33	17	15-20	33	29-38	50	48-52	4	4- 4
80	32	44	40-48	31	23-34	25	20-37	2	1- 3
90	32	43	23-49	28	24-30	29	20-43	3	3- 3
100	29	14	10-19	38	30-42	48	45-51	5	4- 6

[1] MLT—mean low tide.

A 15-foot bank which borders the vegetation zone of A serves as a local source of sediments. B is affected only by indirect sedimentation because the bulkhead and grass restrict erosion. Sediments are brought to this area by currents and wind-driven waves.

Bottom temperatures and salinities from each of the three zones (shore, 50, and 100 feet offshore) of areas A and B were usually identical. When differences between the two areas did occur, they never exceeded more than 2C or 2ppt salinity. The observed temperature range was 14-33C at A and 14-32C at B. The two areas each had a salinity range of 8-20ppt.

COMPARISON OF CATCHES IN NATURAL AND ALTERED AREAS

Area A yielded 75% of 1,532 shrimp *(P. aztecus* and *P. setiferus)* collected from the two areas (Table 2). About 2.5 times more *P. aztecus* and 12.5 times more *P. setiferus* were taken at A than at B. Area A also accounted for 76% of the postlarval and 64% of the juvenile stages of *P. aztecus*. The abundance of *P. setiferus* showed an even more marked difference between A and B. Ninety-six percent of the postlarval and 87% of the juvenile stages of *P. setiferus* collected during this study were taken at A.

TABLE 2

Distribution of brown and white shrimp by area and stage of development

Species and stage	Area A Number	Area A Percent	Area B Number	Area B Percent	Total Number
Brown					
Postlarval	636	76	203	24	839
Juvenile	270	64	155	36	425
Total	906	72	358	28	1,264
White					
Postlarval	157	96	6	4	163
Juvenile	91	87	14	13	105
Total	248	93	20	7	268
Total	1,154	75	378	25	1,532

The number of shrimp captured along each zone — shore, 50, and 100 feet offshore in each area — revealed that the natural shoreline of A was the more productive (Table 3). This concentration of shrimp along the shore of A held for both species, but was particularly evident for white shrimp. Ninety-eight percent of the white shrimp captured at A were from the shore zone. Grouping the catch data by shrimp stages showed that distribution of postlarvae and juveniles was comparable to that noted for the species as a whole.

The distribution of postlarval brown shrimp of area B followed the same general pattern as that in area A, but numbers were fewer (Table 3). Juveniles of this species, however, were equally distributed along the shore and 50-foot zones of B. Almost all of the 358 shrimp collected from the three zones of B were brown shrimp; only 20 white shrimp were caught (Table 3). Although numbers were fewer, most of the postlarval and juvenile white shrimp were captured 100 feet from shore at B.

BIOLOGICAL AND ECOLOGICAL IMPLICATIONS

The significance of estuaries in the life cycle of white shrimp has been discussed by various workers (Weymouth, Lindner, and Anderson, 1933; Anderson, King, and Lindner, 1949; and Pearson, 1939).

TABLE 3

Distribution of brown and white shrimp in relation to distance from shore and stage of development

		Number of Shrimp Captured Per Zone		
Area	Species and Stage	Shore	Offshore (50 feet)	Offshore (100 feet)
A	Brown			
	Postlarval	467	89	80
	Juvenile	185	54	31
	Total	652	143	111
	White			
	Postlarval	154	2	1
	Juvenile	89	1	1
	Total	243	3	2
	Total	895	146	113
B	Brown			
	Postlarval	109	64	30
	Juvenile	63	54	38
	Total	172	118	68
	White			
	Postlarval	1	0	5
	Juvenile	2	4	8
	Total	3	4	13
	Total	175	122	81
Grand Total		1,070	268	194

It is known that *P. setiferus* spawns in the saline offshore waters. The larvae develop in the open sea, then migrate to the estuarine waters where they adopt a benthic existence along the marginal areas. They remain in the brackish estuaries until they approach maturity, then return to the sea. Less is known about the life history of *P. aztecus*, but it is assumed that the life history of this species is similar to that of *P. setiferus* (Baxter, 1962; Chin, 1960; and Williams, 1965).

Since estuaries are the nursery areas for commercially important shrimp, it is necessary to evaluate accurately the effects of man's increasing activities on the suitability of these areas for young shrimp. The present study illustrates one way in which structural modification of estuaries may have detrimental effects. Comparison of the biological, hydrological, and physical data collected reveals similarities and differences between the unaltered and altered habitats in relation to small shrimp captured. Bottom-water temperatures and salinities were similar at all locations studied. Differences in the abundance of small shrimp, therefore, cannot be attributed to these factors.

100-Foot Zones

Shrimp yields, total organic materials, water depth and sediment types were similar at the 100-foot zones of areas A and B. These were the only two zones in which all characteristics measured were similar, including the relative abundance of shrimp.

50-Foot Zones

The 50-foot zones yielded comparable numbers of shrimp. Organics were low but similar, whereas water depths and sediment compositions differed. These differences evidently were not sufficient, however, to influence the number of shrimp occupying these zones.

Shoreline Zones

The environment of the two shoreline zones differs greatly. It is here that differences in the population of brown and white shrimp are truly significant. The natural shoreline harbors considerably more shrimp than the bulkheaded shoreline.

The organic content is much higher at A than at B, water depth is much less, and there is a lush growth of *Spartina alterniflora*. Sediments are similar at both zones. The shallow, tide-influenced waters at A permit the vegetation to flourish. This vegetation in turn contributes to the high organic content of the sediments. The bulkhead at shoreline B causes a deep-water zone which prevents emergent vegetation from growing.

The shore substrate of A resembles the material which Williams (1958) found satisfactory for shrimp. Although his experiments were confined to laboratory tanks, he found brown and white shrimp most frequently on the softer, muddier substrates — loose peat, sandy mud, and muddy sand. Because no penetrometer measurements were made for sediment densities or compactness at A or B, it is impossible for me to describe this characteristic accurately. Yet, the substrate I found supporting the most shrimp was primarily an organic mat mixed with sand-silt-clay.

Loesch (1965) recently presented field data indicating differences in the natural distribution, with respect to water depth and organic debris, of the two commercial species, *P. aztecus* and *P. setiferus*. He located young shrimp of each species concentrated in shallow waters among attached vegetation and in areas with large amounts of organic debris.

Area A: Summary Appraisal

The natural shoreline harbored significantly more brown and white shrimp than the 50- and 100-foot zones. Furthermore, consistently more small shrimp were caught at the natural shoreline than at any of the zones of B. The occurrence of these specimens indicates that the natural shoreline was the preferred habitat (of those sampled) for young shrimp.

Area B: Summary Appraisal

More postlarval brown shrimp were caught at the bulkheaded shoreline than 50 and 100 feet offshore. Juvenile brown shrimp, however, were equally distributed. So few white shrimp were captured in this area that it evidently did not provide a suitable habitat for this species.

CONCLUSION

The distribution of large numbers of small brown and white shrimp along the natural shoreline in preference to the bulkheaded shoreline was not random. Results of this study indicate that the physical nature of a shoreline may significantly affect its biological suitability for young shrimp. For example, the porous nature and high organic content of the natural substrate at station A may provide both shelter and food. It is evident, therefore, that estuarine shorelines must remain in their natural state if they are to support large numbers of young shrimp.

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Efficiency of a Combined Electrode and Louver Array in Guiding Juvenile Steelhead Trout (*Salmo gairdneri*)

INTRODUCTION

In the past several decades, biologists and engineers have been developing methods for diverting fish migrating downstream through hazardous areas created by water-use projects. Many guiding techniques were tried with varying degrees of success. Electrical guiding and deflection with louvers were partly successful, but both systems have limited application.

Electrical guiding, with the advantage of minimal equipment in the water to interfere with the passage of debris, is most successful in low water velocities. Conversely, louvers are effective at higher velocities, but the need for rather closely spaced elements adds to the debris problems and total cost. Bates and Jewett (1961) reported that with a spacing of 5.1 cm the fish-guiding efficiency of a particular louver system was 98%. When the spacing was increased to 25.4 cm, the efficiency decreased to about 63%. This decrease led researchers to seek a method of increasing efficiency without reducing the unobstructed space between louver elements.

Our objective was to determine if the guiding efficiency of a louver system with widely spaced slats would be materially increased by applying electrical energy so that the slats would also function as electrodes.

MATERIALS AND METHODS

The experiment was conducted in April and May 1962 in the Maxwell Irrigation Channel (a diversion of the Umatilla River) near Hermiston, Oregon. Juvenile steelhead trout (*Salmo gairdneri*) migrating downstream were the principal fish available during these tests.

Facilities.—The facility, similar to that of Bates and Jewett (1961) consisted of a concrete-lined flume—15.2 m long, 4.6 m wide, and 1.5 m deep and a similar, but unlined, bypass channel contiguous to the flume. The flume was divided lengthwise by a wooden partition that separated it into two sections, one 1.5 m wide and the other 3 m wide. The 1.5 m channel was not used during this study.

TABLE 1.—*Comparison between the fish-guiding efficiencies (expressed in percent guided) of louvers spaced at 12.1, 25.4, and 40.6 cm with power on and off*

Louver-slat spacing (centimeters)	Power condition	Percent efficiency[1]					Number of fish tested
		Test 1	Test 2	Test 3	Test 4[2]	Average	
12.1	On	82.9	88.5	76.6	—	82.7	471
	Off	84.3	83.9	85.0	—	84.4	408
25.4	On	74.4	82.7	80.3	—	79.1	1,246
	Off	77.9	90.4	41.1	—	69.8	481
40.6	On	19.0	53.8	77.3	53.6	50.9	390
	Off	41.7	66.9	49.2	67.2	56.3	530
Number of fish tested	—	455	1,936	815	320	—	3,526

[1] Number of fish in bypass trap divided by total number of fish captured during each test.

[2] The 40.6 cm spacing was the only spacing tested four times.

A line of vertical louvers, 9.1 by 1.5 m, was placed in the 3 m flume at an angle of 20° to the flow. Each slat was made from sheet steel, about 0.254 cm thick and 7.62 cm wide, held in position by slotted wooden cross members that accommodated the varied spacings. Three spacings were tested: 12.1, 25.4, and 40.6 cm.

Fyke nets screened the entire flow at the downstream end of the canal and captured fish that escaped through the louvers. Fish deflected by the louvers passed through a 15.2 cm-wide bypass to an inclined-screen fish trap.

Application of electrical energy.—When the metal louver slats were energized, each slat functioned as an electrode immersed in a conductive medium. Alternate slats were wired positive or negative, each energized with pulsed direct current at a rate of 15 pulses per second. Each pulse lasted 20 milliseconds. Relatively uniform voltage gradients in the water were obtained by varying the applied voltage from 60 volts at the 12.1 cm spacing to 90 volts at the wider spacings. The resistivity of the water varied from 5,900 to 18,000 ohm cm and averaged 9,600 ohm cm. The electronic equipment used to control the electrical pulses was the same as described by Volz (1962).

To determine the effect of electricity, a louver spacing was tested with the electrical power on for a day and off the following day. Testing was arranged so the data could be treated by analysis of variance. During the 20-day experiment, each louver spacing was tested at least 3 days with the power on and 3 days with power off.

Procedure.—Each experimental day (which began at 8 a.m. and terminated shortly after midnight) consisted of about twelve 1-hour operational periods. At the end of each period the traps and nets were raised, and the fish were removed and counted. As soon as the traps and nets were emptied, they were returned to fishing position and a new period started. The water velocity, temperature, turbidity, and resistivity were measured and recorded every 4 hours; velocity was maintained at about 0.762 m per second.

Fish-guiding efficiencies (%) were determined by dividing the number of steelhead caught in the bypass trap by the total number captured (bypass and fyke nets). Percentages were then converted to arcsin ÷ percentages (Snedecor, 1956) for statistical analysis.

EFFICIENCY IN GUIDING FISH

During the 20-day testing period, 3,526 juvenile steelhead trout were captured. Fork lengths of these fish ranged from 120 to 270 mm and averaged 177 mm. Guiding efficiencies (Table 1) with the power on and off did not differ significantly at the 5% level among the various louver spacings. Similarly, no interaction could be demonstrated between the power conditions and spacing. Analysis of variance did, however, indicate a significant difference between the grand average efficiencies obtained at the three louver spacings tested (83.5% at 12.1 cm; 74.5% at 25.4 cm; and 53.6% at 40.6 cm).

Visual examination of graphs prepared from our data on water temperature, resistivity, turbidity, and weather for possible effects on guiding efficiencies, indicated no correlations.

Test results under the conditions of this field study, although not particularly encouraging, do not eliminte consideration of combining electrical guiding and deflection by louvers.

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Nomenclature of the Spotted Triggerfish, *Balistes punctatus*, of the Eastern Atlantic

DONALD MOORE

NOMENCLATURE OF THE SPOTTED TRIGGERFISH, *BALISTES PUNCTATUS*, OF THE EASTERN ATLANTIC.—In reviewing the systematics of Balistidae in the western Atlantic, I discovered that the earliest name applicable to the spotted triggerfish of the eastern Atlantic is *Balistes punctatus* Gmelin 1788. I also determined that *Balistes forcipatus* Gmelin 1788 is synonymous with *B. capriscus* Gmelin 1788. The name *B. forcipatus* has been used for the spotted triggerfish of the eastern Atlantic, and on several occasions has been applied to specimens from the western Atlantic.

Apparently *B. punctatus* is confined to the eastern Atlantic. Records of its occurrence in the western Atlantic are based either on the type descriptions of *B. spilotopterygius*

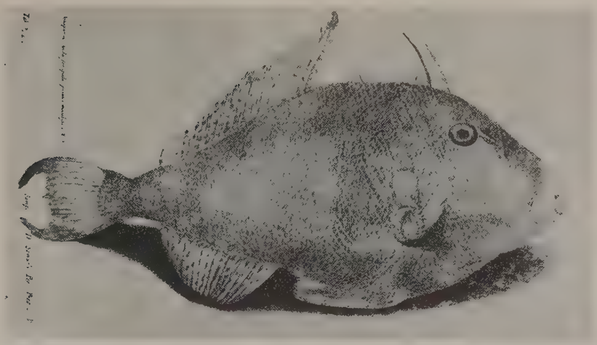

Fig. 1. Photograph of *Guaperva cauda forcipata* (=*B. capriscus*), from Willughby (1686: pl. I22).

Walbaum, *B. powelli* Cope, or *B. moribundus* Cope which Jordan and Evermann (1898:1702) listed as junior synonyms of *B. forcipatus,* or on the belief that the type specimen of *B. punctatus* was taken in the West Indies. I have not been able to determine the type locality of *B. punctatus.*

Balistes punctatus Gmelin, 1788
Spotted triggerfish

Balistes punctatus Gmelin, 1788:1472, after stipvisch *in:* Nieuhof, 1682:274–275 (locality not given).
Balistes guttatus Walbaum, 1792:467 (locality not given).
Balistes ciliaris Bloch and Schneider, 1801: 471 (locality not given).
Balistes radiata Bowdich *in:* Bowdich, 1825: 233, fig. 45 (St. Jago Island).
Balistes dicrostigma (Guichenot) Duméril, 1861:261 (Gorée) *nomen nudum.*
Balistes liberiensis Steindachner, 1867:9–11, fig. 3 (Monrovia).

B. punctatus Gmelin is the first available name given to the eastern Atlantic *Balistes* that has many dark round spots on the body and several filamentous rays in the second dorsal fin. The description of stipvisch (misprinted stipvis) *in:* Nieuhof (1682:274) resembles the eastern Atlantic spotted *Balistes* that has been incorrectly called *B. forcipatus* by many authors. The illustration given by Willughby (1686:pl. I22, see Fig. 1), to which Gmelin (1788:1472) referred in describing *B. forcipatus,* is of *B. capriscus.* Stipvisch (= *B. punctatus*) was described again and illustrated by Nieuhof *in:* Willughby (1686:append. p. 7, pl. 9, fig. 4, see Fig. 2).

The description of *B. ciliaris* Bloch and Schneider, is a composite that refers to *Guaperva etc.* of Lister *in:* Willughby (1686: append. p. 21) and Willughby (1686:pl. I22) as well as to stipvisch *in:* Nieuhof (1682: 274). However, the pectoral fin ray counts (13/13) given for *B. ciliaris* are referable to *B. punctatus,* not *B. capriscus. B. radiata* Bowdich and *B. liberiensis* Steindachner both have descriptions and illustrations referable to *B. punctatus.* LeDanois (1961:515) iden-

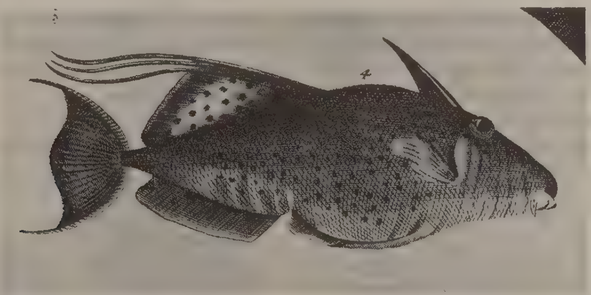

Fig. 2. Photograph of *Stipvisch* (=*B. punctatus*), from Willughby (1686: Appendix pl. 9, fig. 4).

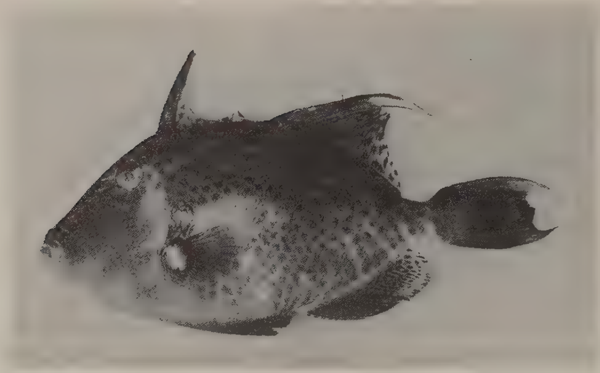

Fig. 3. *Balistes punctatus*, adult, 193 mm SL (USNM 197498).

tified the specimen of *B. dicrostigma* Guichenot as *B. forcipatus* (= *B. punctatus*). *Nematobalistes* Fraser-Brunner (1935:661) was supposedly distinguished from *Balistes* by the elongated second dorsal rays. I follow most subsequent authors in regarding it as a junior synonym of *Balistes*.

Balistes punctatus has a generally gray body with rounded dark or blue spots covering most of the body posterior to the eye (Fig. 3). On fresh adult specimens (Fig. 3), dark or light smaller spots may be found on the cheeks and snout (see also Poll, 1959: fig. 81, pl. 7). About five light lines radiate antero-ventrally from the eye, and two curved light lines extend backward and downward across the snout just back of the mouth. An area posterior to the gill slit lacks spots or lines. The area anterior and ventral to the pectoral base, that also lacks spots or lines on the specimen illustrated in Fig. 3, had about eight vertical light lines on a fresh specimen illustrated by Poll (1959:pl. 7, figs. 1, 2). The vertical wavy lines immediately above the anal fin base on Fig. 3 are more pronounced on Poll's illustrations. A large dark saddle is often present over the dorsal portion of the caudal base. Dark spots are present on the dorsal and anal fins, and the dorsal and ventral margins of the caudal fin, but are absent from the pectoral. The caudal has a vertical light band near its distal end. In smaller juveniles the radiating and curved lines on the head are present, but the dark spots on the side are less numerous.

The anterior end of the second dorsal fin is elevated and in adult specimens the second through the sixth fin rays are elongated—three or four are filamentous and separated (Fig. 3). The anterior part of the anal fin is not elevated. This combination of adult characters is diagnostic of this species. In small juveniles, the anterior rays of the second dorsal fin are slightly produced, but none is elongated or separated. The number of pectoral rays is consistently lower (13/13 or 12/13) than in other *Balistes* species studied in the western Atlantic [a few *Balistes capriscus* have 13/14 pectoral rays] (Moore, in press).

The known range of *B. punctatus* is the eastern Atlantic, the Madeira, Canary, and Cape Verde islands, and along the coast of West Africa from Spanish Sahara to Angola.

I am grateful to those who assisted me in this study. Specimens were made available by: James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Warren G. Freihofer, Stanford University (SU); and Leonard P. Schultz, U. S. National Museum (USNM). James E. Böhlke furnished the photographs in Figs. 1 and 2 and George C. Miller the photograph in Fig. 3. Frederick H. Berry and Jack W. Gehringer gave many helpful suggestions on the manuscript.

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TRIGGERFISHES (BALISTIDAE) OF THE WESTERN ATLANTIC[1]

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ABSTRACT

The significant external characteristics of the six species of triggerfishes (family Balistidae) which occur in the western Atlantic (*Balistes capriscus, B. vetula, Melichthys niger, Xanthichthys ringens, Canthidermis maculatus,* and *C. sufflamen*) are discussed and compared. Synonymies, illustrations, and range of each species, and a key to distinguish them are presented.

INTRODUCTION

Six species of the family Balistidae occur in the western Atlantic Ocean: *Balistes capriscus, Balistes vetula, Melichthys niger, Xanthichthys ringens, Canthidermis maculatus,* and *Canthidermis sufflamen.* This study was made to clarify their descriptions and nomenclature and to facilitate the identification of specimens. The most useful keys and comparative descriptions for the Balistidae of this region—Jordan & Evermann (1898: 1698-1712), Beebe & Tee-Van (1933: 233-237, 314), and Fraser-Brunner (1935: 658-660), the last a key to genera only—are frequently inadequate.

The six species are redescribed and illustrated to delineate (1) many of the significant external changes which take place during development from early juveniles to adults, and (2) characters, such as fin-ray counts, which remain stable throughout this period of development. Counts of the rays of three fins, proportions of ten body parts, and 13 other characters are compared for the six species. A key to facilitate the identification of juveniles and adults is included.

Most of the data were obtained from western Atlantic specimens, but some data from eastern Pacific material were used to assist in clarifying the species taxonomy and to help in analysis of a character that appeared useful for separation of the genera (distance from eye to first dorsal spine). I also used data from a study of eastern Pacific Balistidae by Berry & Baldwin (1966).

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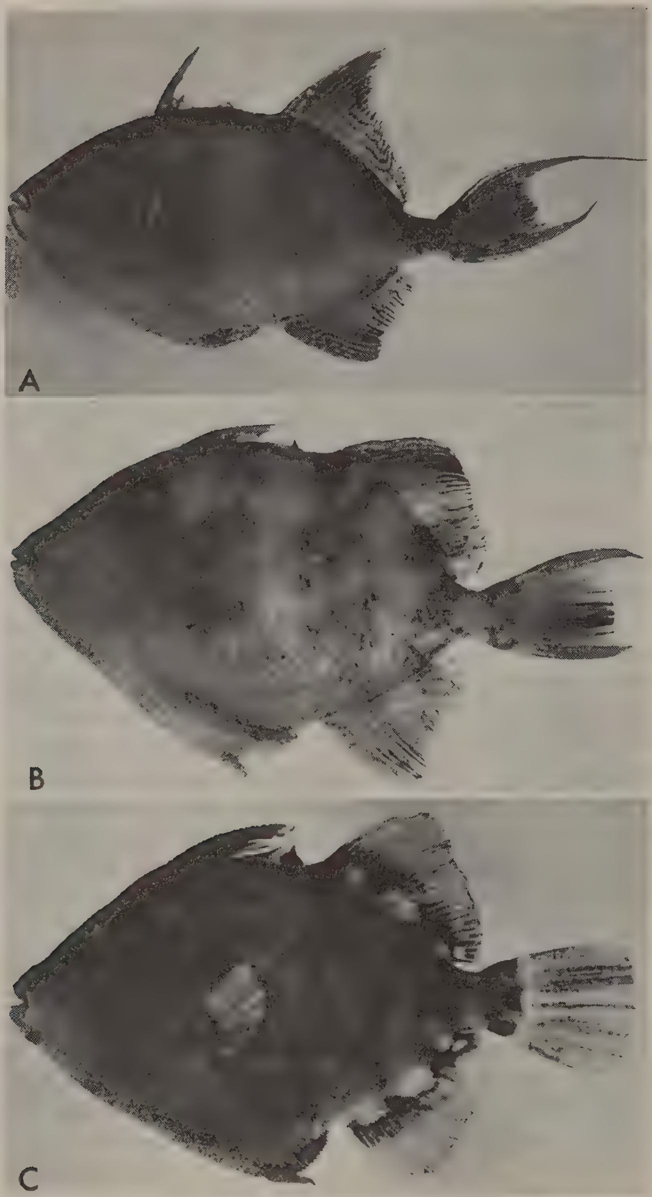

Figure 1. *Balistes capriscus*, gray triggerfish. A, adult, 255 mm SL (TABL, Silver Bay 3757); B, juvenile, 116 mm SL, (TABL, Silver Bay 2525); C, juvenile, 46.1 mm SL (TABL, Silver Bay 4344).

Museum of Comparative Zoology at Harvard University; Warren G. Freihofer, Stanford University; William H. Krueger, Boston University; Jeff W. Moore, Dallas Aquarium; John E. Randall, formerly of the University of Puerto Rico; C. Richard Robins, Institute of Marine Sciences, University of Miami; Richard H. Rosenblatt, Scripps Institution of Oceanography; Leonard P. Schultz, U. S. National Museum; Royal D. Suttkus, Tulane University; Boyd W. Walker, University of California at Los Angeles; F. G. Wood, formerly of Marineland, Florida; and Loren P. Woods, Chicago Natural History Museum. John E. Randall provided the photograph used in Figure 9A. John C. Briggs provided some information concerning the literature. Frederick H. Berry and Jack W. Gehringer gave advice, assistance, and data for this study, and George C. Miller advised and assisted in the photography. M. Jo Knight assisted with the data processing, and Daniel Patlan made the illustrations.

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Balistes capriscus Gmelin, 1788
Gray triggerfish
Fig. 1

Balistes carolinensis Gmelin, 1788: 1468 (Carolinas, U.S.A.).
Balistes capriscus Gmelin, 1788: 1471 (American ocean; excluding references to Indian Ocean).
Balistes forcipatus Gmelin, 1788: 1472 (Brazil: after Guaperva cauda forcipata, etc., by Lister *in* Willughby, 1686: App. p. 21, and Willughby 1686: pl. I-22).
Balistes spilotopterygius Walbaum, 1792: 455 (Brazil).
Balistes buniva Lacépède, 1803: 669, pl. 21 (Nice, France).
Balistes caprinus Valenciennes, 1836-44: 94, pl. 16 (Canaries).
Balistes fulginosus DeKay, 1842: 339, fig. 188 (New York).
Balistes taeniopterus Poey, 1860: 326 (Cuba).
Balistes powellii Cope, 1870: 210 (Newport, Rhode Island).
Balistes moribundus Cope, 1871: 478 (St. Martin, West Indies).

The name *Balistes capriscus* Gmelin is used instead of *B. carolinensis* Gmelin, because *B. capriscus* was selected by the first reviser (Daudin *in* Cloquet, 1816: 476-477). *B. buniva* Lacépède is retained in the synonymy of *B. capriscus* as Briggs (1961: 554) recently suggested; some recent authors have considered it a senior synonym of *Melichthys niger* or *M. piceus* (Fowler, 1936: 1091; Gosline & Brock, 1960: 343). *Balistes forcipatus* Gmelin is a junior synonym of *B. capriscus*. Instead of describing *B. forcipatus*, Gmelin cited a description by Lister in Willughby (1686:

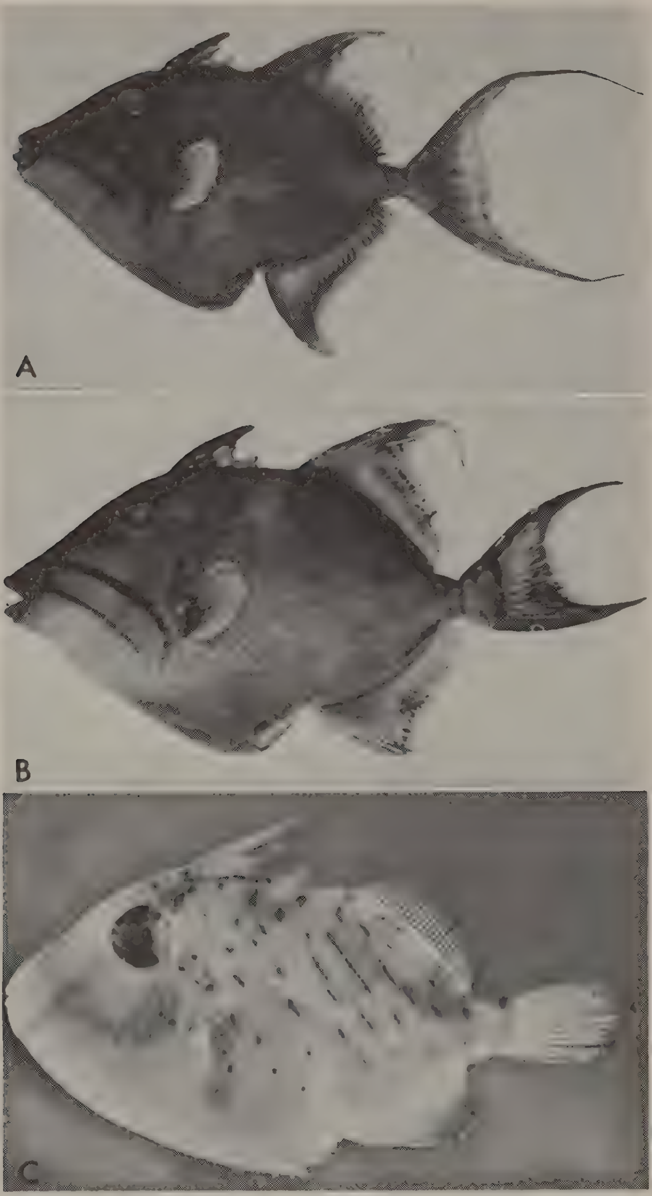

Figure 2. *Balistes vetula*, queen triggerfish. A, adult, 225 mm SL (TABL, Oregon 3563); B, juvenile, 176 mm SL (BLBG, Silver Bay 3479); C, juvenile, 36.0 mm SL (ANSP 72750).

Append. p. 21) and an illustration in Willughby (1686: pl. I-22), both of which are of *B. capriscus*. *Balistes forcipatus* has been used by most authors to refer to the spotted triggerfish of the eastern Atlantic, the correct name of which is *Balistes punctatus* Gmelin, 1788 (Moore, 1967). Three other names have erroneously been placed in junior synonymy of *B. forcipatus* (of authors) relating it to the western Atlantic, but all of these are junior synonyms of *B. capriscus*. *B. spilotopterygius* Walbaum is another redescription that referred to the same description by Lister in Willughby (1686: Append. p. 21) and illustration in Willughby (1686: pl. I-22). *B. powellii* Cope, and *B. moribundus* Cope are both juveniles of *B. capriscus* which have variable color patterns.

Balistes vetula Linnaeus, 1758
Queen triggerfish
Fig. 2

Balistes vetula Linnaeus, 1758: 329 (Ascension Island: after Balistes vetula in Osbeck, 1757: 294).
Balistes bellus Walbaum, 1792: 467 (West Indies).
Balistes equestris Gray, 1854: 31-32 (America).
Balistes vetula trinitatis Nichols & Murphy, 1914: 265 (Trinidad).

The synonymies for this species have remained the same for many years.

Melichthys niger Bloch, 1786
Black triggerfish, Black durgon
Fig. 3

Balistes nigra Osbeck 1757: 295 (pre-Linnaean; Ascension Island).
Balistes niger Bloch, 1786b: 27, pl. 152, fig. 2 (plate incorrectly labeled *Balistes ringens*; China Sea).
Balistes ringens (*non* Linnaeus), Osbeck, 1765: 386 (Ascension Island).
Balistes radula Solander *in* Richardson, 1848: 21, pl. 6, figs. 1-4 (Pacific).
Balistes kibitar Thiollière, 1857: 216 (Woodlark Island).
Balistes piceus Poey, 1863: 180-181 (Cuba).
Balistes buniva (*non* Linnaeus), Günther, 1870: 227-228 (Atlantic, Indian, and Pacific oceans).
Melichthys bispinosus Gilbert, 1890: 125 (Revillagigedo Islands).
Balistes fuscolineatus Seale, 1901: 9 (Honolulu, Hawaii).

Melichthys niger Bloch is the earliest available name. Berry & Baldwin (1966) considered it to be the valid name of this species. I have concluded from examination of specimens that the western Atlantic and eastern Pacific populations of *Melichthys* are one species, and, therefore, record the Atlantic *Melichthys piceus* (Poey) and the Pacific *M. radula* (Solander) as synonyms, as many recent authors have done. *Balistes buniva* or *Melichthys buniva* (of authors) has frequently been used as the senior synonym for this species; as previously stated, however, *Balistes buniva* Lacépède is a junior synonym of *B. capriscus*.

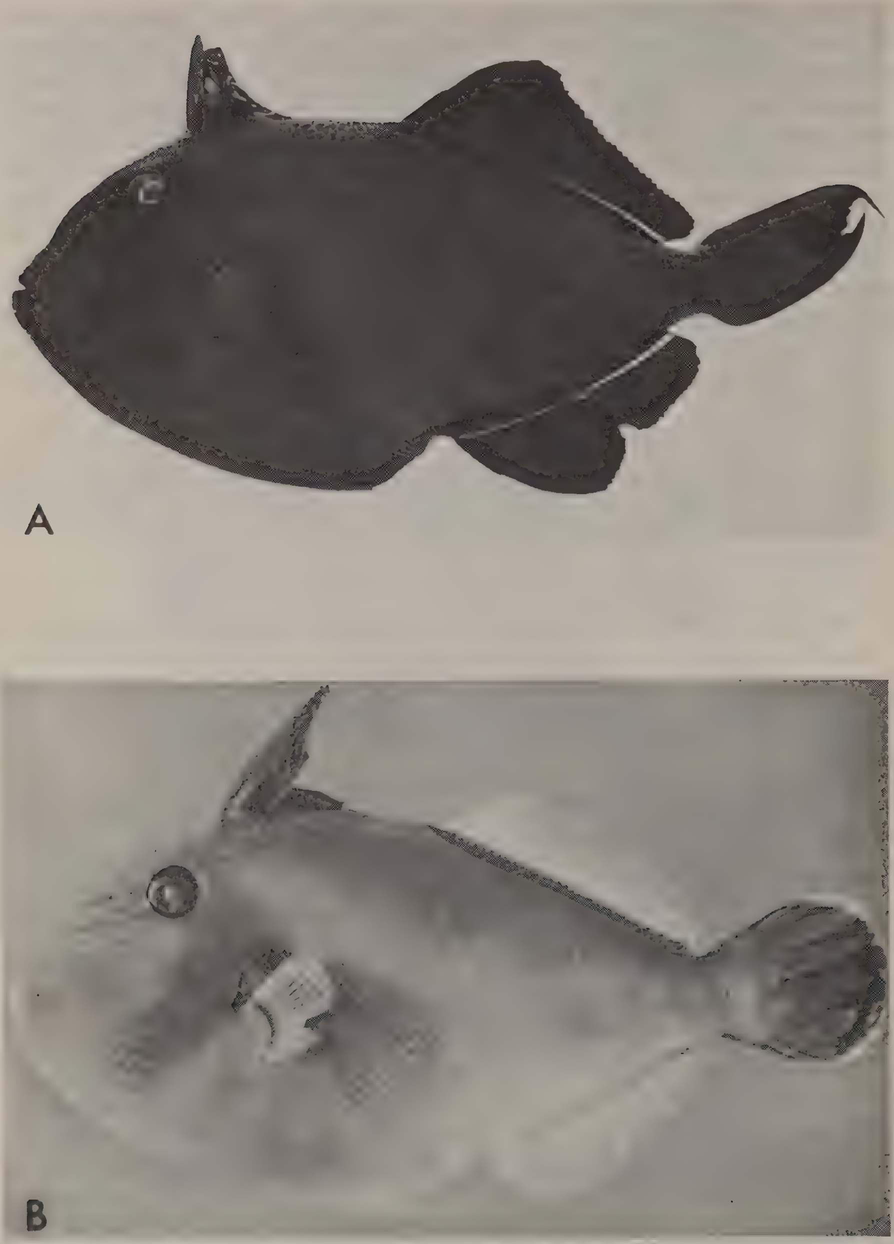

FIGURE 3. *Melichthys niger*, black triggerfish. A, adult, 179 mm SL (BU, CRAWFORD Cruise 10, 14 March, 1957); B, juvenile, 93.5 mm SL (TABL, OREGON 4987).

Xanthichthys ringens (Linnaeus, 1758)
Sargassum triggerfish, Redtail triggerfish
Fig. 4

Balistes ringens Linnaeus, 1758: 329 (locality not clearly indicated).
Balistes curassavicus Gmelin, 1788: 1472 (Curaçao).
Balistes notatus Gray, 1854: 36 (West Indies).
Balistes nitidus Gray, 1854: 36 (American oceans).
Balistes elongatus Hollard, 1854: 71 (Azores).
Balistes cicatricosus Poey, 1860: 327 (Cuba).
Balistes heckeli Müller, 1864: 182 (Mexico).

Several authors (Günther 1870: 221; Gosline & Brock 1960: 342; and Briggs 1961: 554) placed the Pacific *Xanthichthys* in the synonymy of *X. ringens* (Linnaeus). I have concluded they are distinct species since the Pacific *X. mento* has four to six, usually five, horizontal grooves between the scale rows on each cheek and 41-46 scales between the dorsal end of the gill slit and the caudal base, whereas the Atlantic *X. ringens* has three lateral cheek grooves and 38-41 scales.

Canthidermis maculatus (Bloch, 1786)
Rough triggerfish, Ocean turbot
Fig. 5

Balistes maculatus Bloch, 1786a: 202, pl. 152 (American waters).
Balistes americanus Gmelin, 1788: 1473 (America).
Balistes macropterus Walbaum, 1792: 465-466 (America).
Balistes rotundatus Procé, 1822: 130 (Manila Bay).
Balistes angulosus Quoy & Gaimard, 1824: 210 (Hawaiian Islands).
Balistes azureus Lesson, 1830: 121, pl. 10, fig. 2 (New Guinea).
Balistes oculatus Gray, 1832: pl. 90, fig. 1 (India).
Balistes willughbeii Lay & Bennett, 1839: 68, pl. 21, fig. 2 (Acapulco, Mexico).
Balistes adspersus Tschudi, 1845: 31 (Huacho, Peru).
Balistes senticosus Richardson, 1848: 23, pl. 9 (Seas of China).
Balistes brevissimus Hollard, 1854: 56, pl. 3, fig. 1 (New Guinea and Australia).
Balistes longissimus Hollard, 1854: 60, pl. 3, fig. 3 (Vanikoro, Santa Cruz Islands, Society Islands).
Balistes rufus Gray, 1854: 36 (America).
Balistes longus Gray, 1854: 36 (America).
Balistes um Thiollière, 1857: 217 (Woodlark Island).
Balistes minimum Thiollière, 1857: 217 (Woodlark Island).
Balistes melanopterus Cope, 1871: 478 (Darien, Panamá).
Canthidermis viola Herre, 1926: 534, pl. 1 (Sulu Sea).
Canthidermis longirostris Tortonese, 1954: 77-79 (Red Sea).

The type description and illustration given for *Canthidermis longirostris* Tortonese describe very well several formalin-preserved specimens of *C. maculatus* which I examined; they lacked light spots. All other junior synonyms of *C. maculatus* listed have been placed in the synonymy of this species by one or more previous authors.

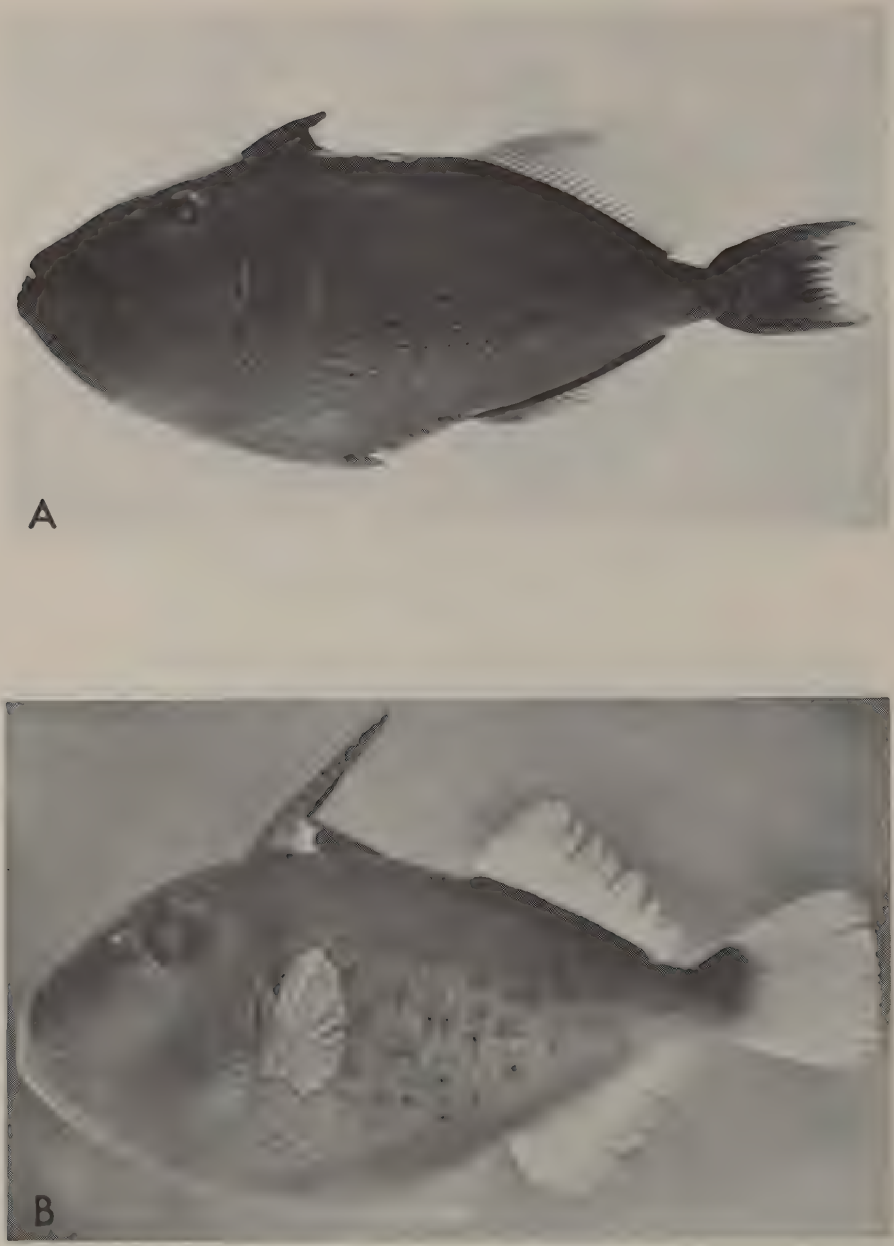

FIGURE 4. *Xanthichthys ringens*, sargassum triggerfish. A, adult, 152 mm SL (ANSP 87891); B, juvenile, 49.6 mm SL (BLBG, GILL Cr. 7, std., 26°20′N, 76°44′W).

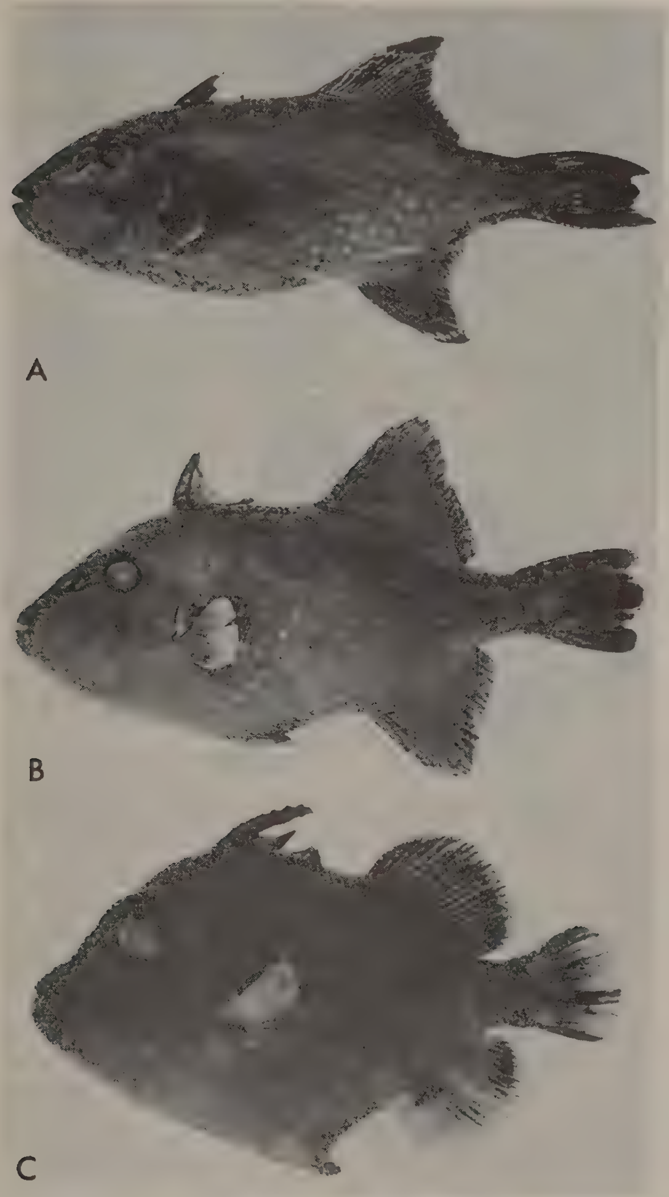

FIGURE 5. *Canthidermis maculatus*, rough triggerfish. A, adult, 315 mm SL (TABL, OREGON 2196); B, juvenile, 145 mm SL (BU, ATLANTIS, 23 November, 1957); C, juvenile, 36.8 mm SL (BU, DELAWARE, 3 September, 1957).

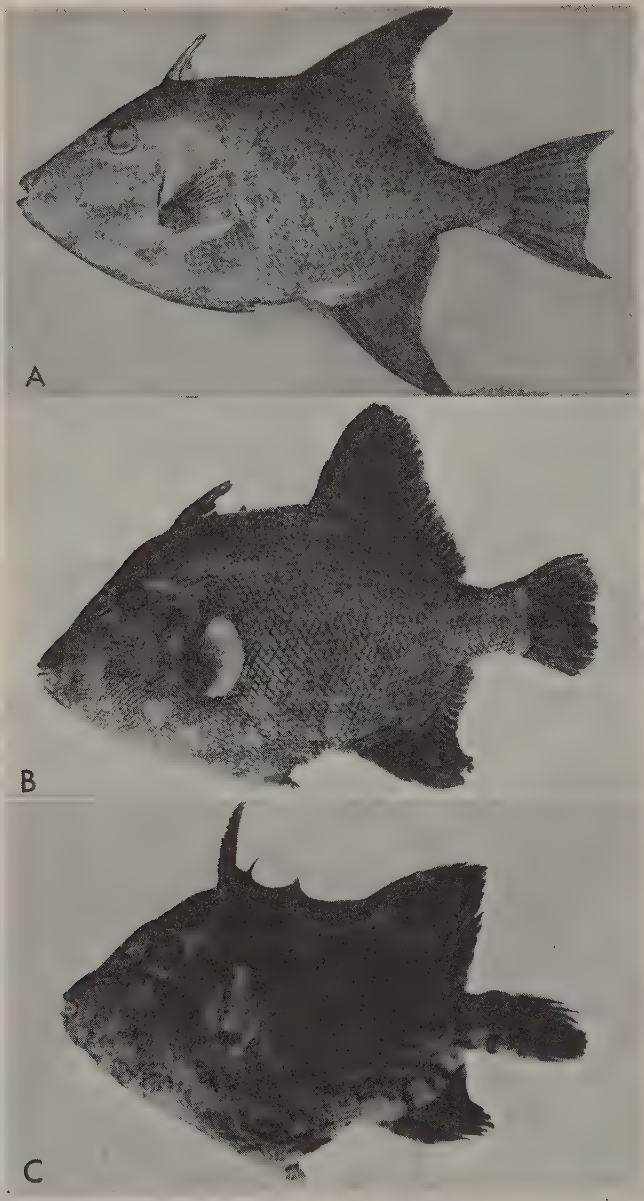

FIGURE 6. *Canthidermis sufflamen*, ocean triggerfish. A, adult, 390 mm SL (UMML, Virgin Islands, sta. 124); B, juvenile, 240 mm SL (TABL, SILVER BAY 423); C, juvenile, 38.7 mm SL (BU, DELAWARE, 3 October, 1957).

Canthidermis sufflamen (Mitchill, 1815)
Ocean triggerfish, Sobaco
Fig. 6

Balistes sufflamen Mitchill, 1815: 467 (New York).
Balistes sobaco Poey, 1860: 324-326 (Havana, Cuba).
Balistes macrops Poey, 1860: 326 (after *Sobaco* in Parra, 1787: 17, fig. 10) (Havana, Cuba).
Balistes asperrimus Cope, 1871: 478 (St. Martin, West Indies).

Canthidermis sobaco is placed in synonymy of *C. sufflamen,* as I was unable to distinguish two distinct forms in a large number of specimens examined. Jordan & Evermann (1898: 1706), in describing *Canthidermis sufflamen*, said it "Differs from *Canthidermis sobaco* in the larger eye, which is 3 in the oblique length of snout. Points of dorsal and anal longer, that of dorsal 3 in total length; produced tips of caudal longer, reaching beyond the convex middle of fin. Scales of trunk without median spine or keel. Body more elongate. Dorsal and pelvic spines smoother than in *C. sobaco*; scales generally less rough." I found that these characters, used by many subsequent investigators to distinguish the two nominal species, had wide ranges and overlapped broadly. The characters are, therefore, inadequate for the separation of these two nominal species. The description of *C. sobaco* generally describes juvenile or early adult specimens of *C. sufflamen.*

KEY TO WESTERN ATLANTIC SPECIES OF BALISTIDAE[2]

1A. Two or more enlarged scales or plates immediately posterior to the gill opening, the plates distinctly larger than any other lateral scales on the trunk. Pelvic process with a flexible joint connecting the external exposed part to the remainder of the process lying underneath the skin 2
1B. No enlarged scales or plates immediately behind gill opening, any modified scales present not as large as the other scales on side of body. Pelvic process not flexible, the exposed and internal parts continuous 4
2A. About 8 to 11 horizontal rows of ridged scales bearing anteriorly directed spines along sides of peduncle and area between anal and soft dorsal fins. Anal rays 29-31. Dorsal rays 31-35. Pectoral rays 15-17 .... *Melichthys niger*
2B. No horizontal rows of ridged scales bearing anteriorly directed spines on sides of body and peduncle. Anal rays 23-28 3
3A. Head with two broad, curved, dark or blue bands on cheek, and

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[2] Many characters in the key, other than articulation of pelvic process and numbers of fin rays, may not apply to specimens shorter than 50 mm SL. Data from specimens shorter than 10 mm SL were not included in this study.

several narrow dark or blue bands radiating from eye. Anal rays 27-28. Dorsal rays 29-31. Pectoral rays 14-15. Longest dorsal soft ray 36-71 per cent SL on specimens larger than 150 mm SL .... *Balistes vetula*

3B. Head without prominent dark or blue bands. Anal rays 23-26. Dorsal rays 26-29. Pectoral rays 14-15 (13). Longest dorsal soft rays 23-29 per cent SL on specimens larger than 150 mm SL .... *Balistes capriscus*

4A. Scales on cheek fused together in horizontal rows, between which are narrow and parallel naked areas or grooves. Least distance from eye to first dorsal spine 8-10 per cent SL. Peduncle depth 7-8 per cent SL. Anal rays 23-27. Dorsal rays 26-30. Pectoral rays 13-14 .... *Xanthichthys ringens*

4B. Cheek completely scaled, without horizontal grooves. Least distance from eye to first dorsal spine 12-18 per cent SL. Peduncle depth 10-15 per cent SL 5

5A. Anal rays 20-22. Dorsal rays 23-25. Pectoral rays 13-15. Body depth 36-45 per cent SL on specimens larger than 150 mm SL .... *Canthidermis maculatus*

5B. Anal rays 23-25. Dorsal rays 25-28. Pectoral rays 15-16. Body depth 47-63 per cent SL on specimens larger than 150 mm SL .... *Canthidermis sufflamen*

Analysis of Characters

Pigmentation and Coloration.—The following descriptions of pigmentation and color are of preserved specimens unless stated otherwise.

Balistes capriscus has a generally gray body with four dark patches at the second dorsal-fin base. One patch, a very dark saddle beneath the origin of the second dorsal fin, is distinct on most specimens and remains distinct on specimens preserved for many years; a second, less dark patch lies beneath rays 7-10 of the second dorsal fin; a third, even less dark patch lies beneath rays 18-22 of the second dorsal fin; and a fourth, narrower patch forms a saddle that lies just posterior to the second dorsal fin. Vertically elongated patches of pigment tend to form four irregular vertical bars on each side; one is located above and below the orbit, another below a point between the second and third dorsal spines, a third below the base of the first six dorsal soft rays, and a fourth below the posterior end of the second dorsal base (Fig. 1). The posterior two bars blend with the saddles. These bars are sometimes very faint (Fig. 1A), and usually are more distinct on juveniles (Fig. 1B). Dark lateral reticulations and light spots often occur on the second dorsal and anal fins. The reticulations tend to form dark stripes in the middle and posterior part of the fin. Juveniles less than 50 mm SL have many small, dark, rounded spots and larger, irregular dark patches on the body, and mostly translucent second dorsal-, anal-, and caudal-fin membranes (Fig. 1C). Saddles similar to those on the dorsal fin are also present on the anal fin of early juveniles. The saddles are interspersed with light spots. On live specimens, I have observed quick changes in the intensity of dark pigment in the four vertical bands and the dark reticulations (blue on live specimens) of the dorsal and anal fins.

Balistes vetula has a gray body with two broad, dark bands, and one dark line above them, proceeding posteroventrally from the snout to the vicinity of the pectoral-fin base (Fig. 2A & B). There is another dark band immediately under the lower lip. About eight wavy, dark lines radiate from the eye. The dorsal surface of the eye has about six dark spots. Several wavy, dark reticulations cross the dorsal and anal fins. The distal margins of these fins are light. Vertical dark bands cross the caudal base, and a dark band crosses the caudal rays near the distal margin of the caudal fin. On juveniles below 50 mm SL, dark, broken lines run along some of the anterodorsal to posteroventral diagonal rows of scales on the sides (Fig. 2C); this character is present, but indistinct, on some of the larger specimens (Fig. 2B). The small juveniles also have generally translucent dorsal-, anal-, and caudal-fin membranes. Often the two broad bands which are present above the jaw on larger specimens are indistinct in small juveniles (Fig. 2C). On live and fresh specimens the dark bands and reticulations are blue. Townsend (1929:344, pl. 25), in illustrating color phases of *B. vetula*, noted a dull color pattern, in which the dark diagonal bars along the scale rows were most prominent. He found this pattern on fish during rest as well as during fright.

Melichthys niger has the darkest pigmentation of any adult western Atlantic balistid (Fig. 3A). Recently preserved, small juvenile specimens of *C. maculatus* are also very dark (Fig. 5C). The entire body, including the fins, is black, except for a narrow white band along the second dorsal and anal fins near their bases. The band is slightly broader posteriorly. On many specimens, dark lines which radiate above and before the eye are similar to the lines radiating from the eye on *B. vetula.* The smallest specimen examined, a prejuvenile of 93.5 mm (SL) had a paler body than did the adults; the entire second dorsal and anal fins were translucent instead of dark, and the dorsal and ventral distal margins of the caudal fin were white (Fig. 3B). In aquaria, the adults had a black body with a slight chestnut color on the upper cheek, and blue instead of white stripes near the bases of the second dorsal and anal fins. Randall (1955: 220-221) noted that, when they are living in their natural habitat, specimens of the Pacific *M. niger* have narrow, bright blue lines at the bases of the soft dorsal and anal fins.

Xanthichthys ringens has a generally bronze-yellow hue which, in adults, is lighter on the belly than on the back (Fig. 4A). Most of the side posterior to the head, including the area under the pectoral fin, has distinct dark spots at each junction of four scales. Two of the three horizontal grooves between the scale rows on the cheek contain very dark pigment. The head, belly, and the regions near the dorsal, anal, and caudal bases lack spots. The first dorsal-fin membrane in both adults and small juveniles is very dark except near the bases of the first two spines (Fig. 4B). The second dorsal- and anal-fin membranes are translucent, but their bases are very dark. In small juveniles, the dorsal half of the body is darker than the ventral half, and the large, irregular dark spots on the sides are larger and fewer than on adults (Fig. 4B). Small juveniles lack horizontal cheek grooves. A few spots occur on the side of the head of specimens under 30 mm SL. Fresh specimens of small juveniles are dark gray on the upper half of the side of the body.

Canthidermis maculatus has a gray-to-brown body that is lighter or more buff ventrally (Fig. 5A & B). Usually, many light spots occur on the sides and ventral surface of the body (9-17 spots between the origins of the second dorsal and anal fins) and on the dorsal and anal fins. Spots are numerous, though often less distinct, on the cheeks and throat. Dorsal- and anal-fin membranes are dark and frequently are spotted. Some specimens, including some recently preserved ones, lack spots. On specimens of 10-50 mm SL, the color patterns are darker and the light spots are more irregular (Fig. 5C). Specimens measuring 10-20 mm SL have about three black papillae or small fleshy protrusions just above the lateral line near the peduncle. In all sizes, the first dorsal-fin membrane is dark and the pectoral fin is unmarked. On live specimens (none was examined) the presence of light spots, as in *C. sufflamen*, probably is variable.

Canthidermis sufflamen also has a gray-to-brown body that is lighter or more buff ventrally (Fig. 6A). The dorsal-, anal-, and caudal-fin membranes are dark, and the pectoral fin is mostly unmarked at all sizes (Figs. 6A & B). Specimens measuring less than 100 mm SL have irregular buff to dark-gray or brown spots on the body and over much of the second dorsal, anal, and caudal fins (Fig. 6C). The membrane of the first dorsal fin is dark on the small juveniles. Many small juveniles have three to six small, black papillae or small fleshy protrusions just above the lateral line at the peduncle and below the first dorsal fin. Very small specimens, 10-20 mm in SL, often have dark, laterally elongated oval spots on a light gray background. In an aquarium, a specimen which measured 175 mm SL intermittently exhibited white spots on the posterior half of the body including the second dorsal, anal, and caudal fins. These spots were larger and less numerous than those usually found on preserved specimens of *C. maculatus*. On a specimen captured by dipnet, similar white spots disappeared after the fish was preserved.

Pelvic Process.—In all species of *Balistes* and *Melichthys* examined, the pelvic process (the rays and encasing scales protruding postero-ventrally on the terminal end of the basypterigium) is flexible in a dorso-ventral plane at approximately the point of emergence from the body. The flexibility between the two proximal, encasing, scale segments that allows movement of the distal segments in the dorso-ventral plane was described in detail by Tyler (1962: 227-229). No lateral movement of the pelvic process is possible in any of the species studied. *Canthidermis* and *Xanthichthys* have no flexible articulation between segments of the pelvic process.

Dorsal, Anal, and Pectoral Rays.—As in all species of Balistidae, the first dorsal fins of the six species have three spines. The pectoral fins have a short spine on the dorsal edge of the fin origin, which is prominent in very small juveniles but reduced to a slight knob in adults. Table 1 gives the frequency distribution in each of the six species for the numbers of soft rays in the second dorsal, anal, and pectoral fins. Most specimens were bilaterally symmetrical in numbers of pectoral-fin rays (*B. capriscus*, 95 per cent; *B. vetula*, 87 per cent; *M. niger*, 90 per cent; *X. ringens*, 83 per cent; *C. maculatus*, 83 per cent; and *C. sufflamen*, 84 per cent). The first three species in Table 1 (those with a flexible pelvic process) may be separated from each other by the number of anal rays. The last three species (those having an inflexible pelvic process) may be separated as follows: *C. maculatus* from *C. sufflamen* and *X. ringens* by number of anal rays; and *C. sufflamen* from *X. ringens* by number of pectoral rays.

Profile of Second Dorsal Fin.—On large juveniles and adults of all six species, the anterior part of the second dorsal fin is elevated; the second to seventh rays are the longest. On small juveniles, the longest rays may be as far back as the ninth or tenth. The anterior part of the second dorsal fin is produced in large adult specimens of *B. capriscus, B. vetula, C. maculatus*, and *C. sufflamen.* Adults of *B. vetula* also have several long, filamentous rays in the produced part of the fin (Fig. 2A).

Profile of Anal Fin.—The second to sixth anal-fin rays are the longest on large juveniles and adults of all six species. In adults, the anterior part of the fin is distinctly produced in *B. vetula* (Fig. 2A & B), *C. maculatus* (Fig. 5A & B), and *C. sufflamen* (Fig. 6A & B); it is elevated in *B. capriscus* (Fig. 1A & B) and *M. niger* (Fig. 3) but only slightly elevated in *X. ringens* (Fig. 4A).

Modified Scales on Cheek.—The scales of *X. ringens* in the region between the lower jaw and the gill opening (Fig. 4A) are vertically elongated rectangles or parallelograms. On specimens which measure over 500 mm SL, four rows of these scales are separated by three lateral grooves (Fig. 4A). The two upper grooves are wider and more pronounced than the lower one, which may be indistinct. On specimens which are about 40-50 mm SL,

TABLE 1

FREQUENCY DISTRIBUTIONS OF SOFT RAYS IN SECOND DORSAL, ANAL, AND PECTORAL FINS OF THE SIX SPECIES OF WESTERN ATLANTIC BALISTIDAE

	Dorsal soft rays													Anal soft rays												Pectoral soft rays[1]				
	23	24	25	26	27	28	29	30	31	32	33	34	35	20	21	22	23	24	25	26	27	28	29	30	31	13	14	15	16	17
B. capriscus	—	—	—	2	39	47	6	—	—	—	—	—	—	—	—	—	1	40	46	7	—	—	—	—	—	3	165	7	—	—
B. vetula	—	—	—	—	—	—	5	21	4	—	—	—	—	—	—	—	—	—	—	—	19	11	—	—	—	—	54	6	—	—
M. niger	—	—	—	—	—	—	—	—	1	2	6	9	4	—	—	—	—	—	—	—	—	—	5	8	9	—	—	3	33	6
X. ringens	—	—	—	1	5	8	14	1	—	—	—	—	—	—	—	—	1	3	11	11	3	—	—	—	—	41	13	—	—	—
C. maculatus	8	18	9	—	—	—	—	—	—	—	—	—	—	5	17	13	—	—	—	—	—	—	—	—	—	4	37	26	—	—
C. sufflamen	—	—	4	26	29	3	—	—	—	—	—	—	—	—	—	—	17	38	7	—	—	—	—	—	—	—	—	72	54	—

[1] Includes individual counts on each of both fins of most specimens.

these scale rows are only slightly separated from each other (Fig. 4B). The scale pattern is similar in specimens smaller than 40 mm SL, but without spaces or grooves between scale rows. The other five species lack distinctly modified cheek scales.

Scale Rows on Body.—The irregularity of scale rows on the body makes precise counts of lateral or dorsoventral scales difficult on many juveniles. Counts of the number of anterodorsal to posteroventral scale rows between the dorsal end of the gill opening and the caudal base range as follows: *X. ringens*, 38-41; *C. maculatus*, 42-49; *B. vetula*, 45-51; *B. capriscus*, 48-53; *C. sufflamen*, 49-53; and *M. niger*, 50-57.

Ridges and Spines on Scales.—*M. niger* has eight to eleven horizontal rows of ridged scales, on the sides at the peduncle and between the second dorsal and anal fins, that bear anteriorly directed spines (Fig. 3). No such scale rows were found in the other five species. Each scale on the sides of small juvenile specimens of *B. capriscus, B. vetula, C. maculatus*, and *C. sufflamen* has a single spine. In *B. capriscus* and *B. vetula,* these scale-spines become rudimentary or disappear in specimens measuring 25 to 40 mm SL, and are absent in larger specimens; in *C. maculatus* they are rudimentary by the time individuals reach 200 to 430 mm SL and disappear by the time that 475 mm SL is reached; and in *C. sufflamen* they are usually lacking on specimens over 400 mm SL. The only specimen of *X. ringens* that had scales with spines was an 18.1-mm specimen, the smallest examined; however, the spines were rudimentary.

Lateral Line.—The location of the lateral line is similar in all six species. Lateral-line branches are above and below the orbit. The branches unite just posterior to the orbit to form a single line that proceeds posteriorly, and slightly dorsally, to its dorsalmost position just below the base of the third dorsal spine. From that point, the lateral line proceeds abruptly downward to its ventralmost position, following an anterodorsal to posteroventral, vertical row of scales for about three-fourths of the distance to the anal-fin base; then the line turns abruptly upward and follows an anteroventral to posterodorsal row of scales to the middle of the side, and thence runs posteriorly along the middle of the side to the caudal base. On *M. niger*, the lateral line is often indistinct at or near its ventralmost position. I did not find the lateral line in *B. vetula* to be incomplete, as stated by Jordan & Evermann (1898: 1703).

Modified Scales above Pectoral Fins.—*M. niger* and the two species of *Balistes* have several prominent enlarged scales or plates just above the dorsal end of the pectoral insertion and posterior to the gill opening (best illustrated in Fig. 2B). Two modified scales, of somewhat irregular shape and larger than the other modified scales, are located side by side; there are several smaller modified scales or plates above them. I have found that adult and large juvenile specimens of *X. ringens* have about eight small, modified scales or plates, none as large as the largest normal scales on the trunk. On juveniles smaller than 50 mm SL, these modified scales are as large as, or larger than, normal scales. *X. ringens* has been described previously as having no "osseus plates" above the pectoral fins (Jordan & Evermann, 1898: 1699, 1708-9; Fraser-Brunner, 1935: 658-60). The two species of *Canthidermis* lack modified scales above the pectorals, at any size.

Teeth.—All six species have eight premaxillary and eight dentary teeth. On specimens of *M. niger* of 126 mm SL and larger, these teeth are white, and all are incisors. The premaxillary bone of a 96-mm *M. niger* has one incisor and seven cuspids. All 16 teeth are cuspids on the smallest specimen (93.5-mm SL) examined. The maxillary and anterior dentary teeth of the other five species are cuspids, in all specimens regardless of size.

Vertebrae.—Vertebrae are 7 + 11 in all of the specimens examined in each species (seven specimens of *B. capriscus*, three of *B. vetula*, two of *M. niger*, six of *X. ringens*, eleven of *C. maculatus*, and seven of *C. sufflamen*).

Sexual Dimorphism.—The lower jaw projects antero-ventrally in adult males of *M. niger*, but not in females (Fig. 3A). No sexual dimorphism was observed in the other species.

Body Proportions.—The data for proportional measurements on which the discussion below is based are to be found in Table 2.

SNOUT LENGTH: Snout length is here defined as the least distance from the tip of the snout to the orbit. On specimens longer than 100 mm SL, snout length may be used to separate most specimens of *Balistes* (23-28 per cent SL) from those of *M. niger*, *X. ringens*, and *C. maculatus* (18-23 per cent SL). Snout lengths of *C. sufflamen* (21-23 per cent SL) are less than those in *B. vetula* (26-28 per cent SL) and overlap those of the other four species. On specimens between 10-50 mm SL, the snouts of *B. capriscus, B. vetula, X. ringens, C. maculatus*, and *C. sufflamen* are generally short, usually proportionately the same as those on the larger specimens of *Melichthys*, *Xanthichthys*, and *Canthidermis*.

EYE DIAMETER: The eye diameter is defined as the horizontal diameter inside the orbit. Eye diameter serves to separate some species which occur in the western Atlantic. *Balistes* generally has larger eyes than *Melichthys*, in specimens larger than 100 mm SL. (In the 100- to 200-mm range in SL: *Balistes* = 8-10 per cent SL; *Melichthys* = 7 per cent SL. In the 200- to 300-mm range in SL: *Balistes* = 6-9 per cent SL; *Melichthys* = 5-6 per cent SL.) In specimens larger than 200 mm SL, the eye diameter changes little with further increase in body length.

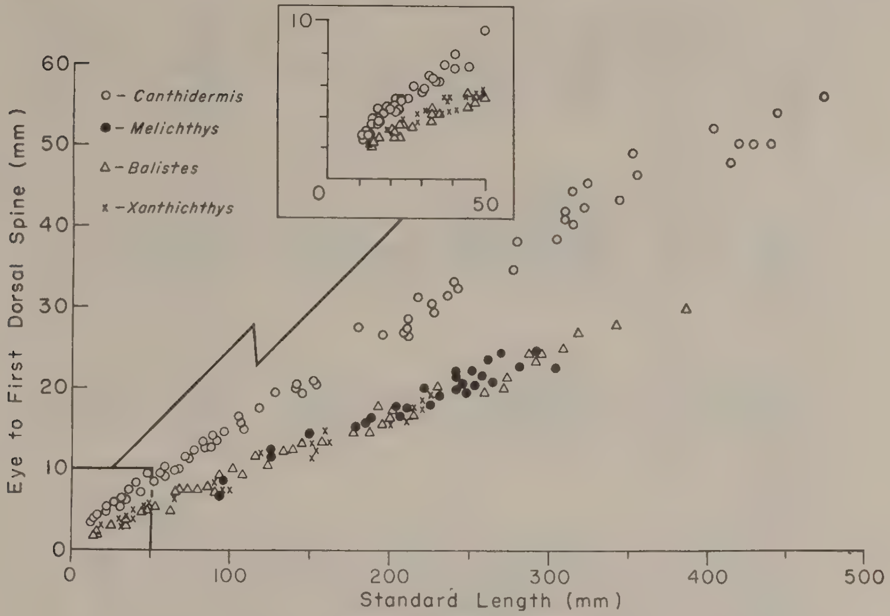

FIGURE 7. Relation between standard length and the distance from eye to first dorsal spine, for *Canthidermis, Melichthys, Balistes,* and *Xanthichthys,* including the Pacific specimens examined.

INTERORBITAL WIDTH: The interorbital width is the least width across the frontal between the orbits. The interorbital width in *Canthidermis* is greater than in *Balistes* and *Melichthys*, for specimens ranging from 50 to 100 mm SL (*Canthidermis*, 14-17 per cent SL; *Balistes* and *Melichthys*, 10-13 per cent SL); and is greater than in all other species, for specimens in the 100- to 200-mm range in SL (*Canthidermis,* 13-16 per cent SL; the other four species, 8-12 per cent SL). In specimens which are over 200 mm SL, *Canthidermis* (11-13 per cent SL) may still be separated from *Balistes* (8-10 per cent SL). Data obtained from examination of the larger Pacific species of *Melichthys* and *Xanthichthys* indicate that the values for interorbital width in specimens larger than 250 mm SL range between those for *Canthidermis* and *Balistes*. For all sizes, interorbital width in *Canthidermis* is generally greater than in *Balistes*. In *X. ringens*, which has a smaller interorbital width as a large juvenile or adult, the width is as great as in *Canthidermis* for specimens whose size is between 20 and 50 mm SL.

DISTANCE FROM EYE TO FIRST DORSAL SPINE: This distance is taken as the least distance from the orbit to the anteriormost insertion of the first dorsal spine. The distance from the eye to the first dorsal spine is greater

TABLE 2

Proportional Measurements for Ten Body and Fin Parts of Western Atlantic Species of Balistidae, in Percentage of Standard Length, by Selected Ranges of Standard Length

	Size range (mm SL)						
	10–20.0	20.1–50	50.1–100	100.1–150	150.1–200	200.1–300	300.1 and over
				Snout length			
B. capriscus	19–21 (4)[1]	18–23 (11)	21–25 (14)	23–25 (9)	23–26 (4)	24–26 (7)	25–26 (2)
B. vetula	20 (1)	21–24 (8)	23–26 (2)	27 (2)	26–28 (6)	26–28 (7)	26 (1)
M. niger	–	–	22–23 (2)	23 (2)	19–20 (3)	21–22 (14)	–
X. ringens	25 (1)	20–25 (16)	20–21 (4)	20–23 (2)	20–21 (5)	–	–
C. maculatus	17–21 (5)	19–22 (5)	20–21 (6)	19–21 (8)	19–20 (2)	19 (3)	18–19 (3)
C. sufflamen	18–23 (16)	18–22 (15)	20–24 (14)	22 (1)	23 (2)	22 (3)	21–23 (10)
				Eye diameter			
B. capriscus	15–18	11–16	10–12	8–10	8–9	6–8	6
B. vetula	15	13–14	10–11	9	8–10	7–9	7
M. niger	–	–	7–8	7	7	5–6	–
X. ringens	16	11–15	9–11	8–10	7–8	–	–
C. maculatus	16–19	11–18	10–11	8–10	8	6	5–6
C. sufflamen	16–19	12–15	9–13	–	7	6–7	6–7
				Interobital width			
B. capriscus	17–19	10–17	11–13	10–11	10	9–10	8–9
B. vetula	20	11–13	10	8–9	8–9	8–10	9
M. niger	–	–	12–13	11	10	10–11	–
X. ringens	20	14–21	11–16	11	9–12	–	–
C. maculatus	24–27	18–22	14–16	13–16	13	12–13	11–12
C. sufflamen	17–22	14–20	14–17	14	14	13	11–13

[1] Number of specimens examined in parentheses.

TABLE 2 (Continued)

	Size range (mm SL)						
	10–20.0	20.1–50	50.1–100	100.1–150	150.1–200	200.1–300	300.1 and over
			Distance from eye to first dorsal spine				
B. capriscus	15–18	11–16	9–11	9–10	8–9	8–9	8
B. vetula	16	10–12	8–10	9	8	7–9	8
M. niger	–	–	9	10	8–9	8–9	–
X. ringens	18	11–16	8–10	8–10	8–9	–	–
C. maculatus	24–28	17–24	15–17	13–16	14	13–14	13–14
C. sufflamen	22–25	16–22	14–18	14	15	13–14	12–14
			Distance from snout to first dorsal spine				
B. capriscus	44–47	38–43	38–41	38–40	36–39	36–39	35–38
B. vetula	45	40–44	41	42	40–42	38–42	37
M. niger	–	–	34–35	34	29–30	30–33	–
X. ringens	50	39–49	34–36	33–35	31–32	–	–
C. maculatus	53–56	41–53	37–44	36–40	36	34–36	32–35
C. sufflamen	51–61	44–51	42–46	42	41	37–39	34–39
			Length of third dorsal spine				
B. capriscus	10–12	7–10	5–8	5–7	5	2–6	5
B. vetula	13	6–11	6–8	4–6	4–7	5	4
M. niger	–	–	1–2	1	0–1	0–2	–
X. ringens	2	0–2	0	0	0–2	–	–
C. maculatus	4–8	2–6	3–6	3–5	2	2	1–2
C. sufflamen	5–8	5–8	4–7	6	5	1–2	0–2

TABLE 2 (CONTINUED)

	Size range (mm SL)						
	10–20.0	20.1–50	50.1–100	100.1–150	150.1–200	200.1–300	300.1 and over
			Length of longest dorsal soft ray				
B. capriscus	16–19	16–22	18–29	20–28	23–28	25–29	26
B. vetula	18	15–23	22–25	29–30	36–50	42–71	50
M. niger	–	–	13	20	20–21	17–22	–
X. ringens	16	14–16	14–20	19–21	18–22	–	–
C. maculatus	17–19	17–21	20–28	22–27	24–26	24–26	22–25
C. sufflamen	16–26	17–26	20–28	–	24	24–36	30–36
			Length of longest anal soft ray				
B. capriscus	17–20	16–18	15–26	20–23	20–23	22–24	21–22
B. vetula	16	14–18	20	22–23	25–27	25–28	24
M. niger	–	–	12	18–20	19–20	16–19	–
X. ringens	17	13–16	14–17	18–19	16–19	–	–
C. maculatus	17–20	17–21	20–25	21–26	24–25	23–24	21–22
C. sufflamen	15–20	16–24	14–26	–	26	25–33	28–35
			Body depth				
B. capriscus	63–70	54–64	52–67	50–63	51–57	48–55	49–51
B. vetula	61	56–64	62	57–59	53–60	52–59	52
M. niger	–	–	50–53	45–58	49–52	48–58	–
X. ringens	64	48–60	49–51	45	42–53	–	–
C. maculatus	64–76	58–70	50–62	46–54	42–45	41–42	36–38
C. sufflamen	63–77	56–70	56–66	54	56–63	55–58	47–54
			Depth at caudal peduncle				
B. capriscus	11–13	11–13	9–12	9–10	9	8–9	8
B. vetula	10	9–10	9	9	8–9	7–9	8
M. niger	–	–	10	10	8–9	9–10	–
X. ringens	9	8–10	8	8	7–8	–	–
C. maculatus	13–19	12–15	11–14	12–14	12	12	10–12
C. sufflamen	12–15	11–14	11–15	13	13	13–14	11–13

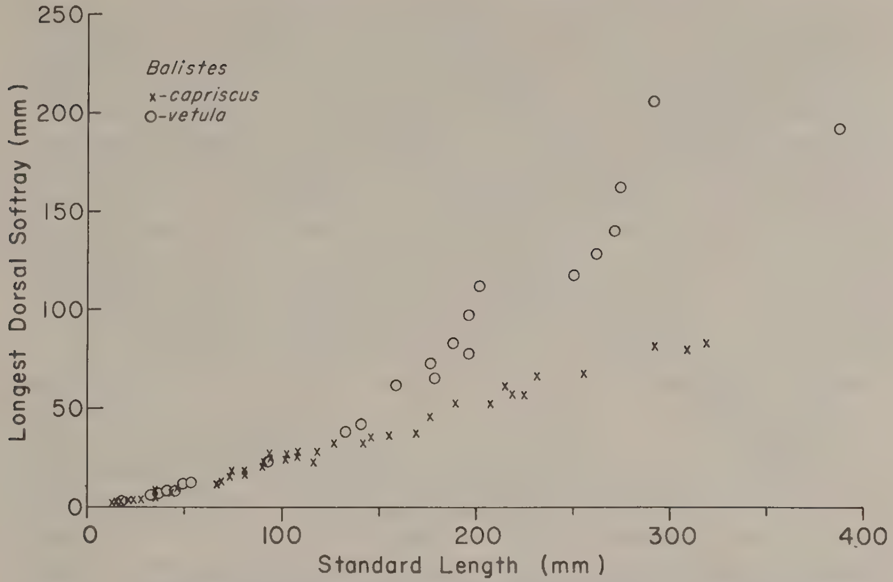

FIGURE 8. Relation of the length of longest dorsal soft ray to standard length, for *Balistes capriscus* and *B. vetula* from the western Atlantic.

in *Canthidermis* than in the other three genera (Fig. 7). In relation to the standard length, the distance from the eye to the first dorsal spine in juveniles decreases with growth. Above the size of 50 mm SL, *Canthidermis* (12-18 per cent SL) may be easily separated from *Balistes, Melichthys* (7-11 per cent SL), and *Xanthichthys* (8-10 per cent SL) by means of this character. From 10 to 50 mm SL, the juveniles of *Canthidermis* are also separable from those of *Balistes* and *Xanthichthys* (Fig. 7).

DISTANCE FROM SNOUT TO FIRST DORSAL SPINE: This distance is measured as the distance from the tip of the snout to the insertion of the first dorsal spine. The distance from the snout to the first dorsal spine, on specimens which are longer than 100 mm SL, is greater in *Balistes* (35-42 per cent SL) than in *M. niger* and *X. ringens* (29-35 per cent SL). The range of values for this distance in *Canthidermis* (32-42 per cent SL) overlaps the ranges for the other species. On specimens which range in size from 10 to 50 mm SL, this distance is about the same in the five species examined, and is proportionately the same, or greater, on large specimens of *Balistes*.

LENGTH OF THIRD DORSAL SPINE: This length is measured as the distance from the top of the first dorsal-fin groove to the tip of the third dorsal spine, when the spine is normally erect. The third dorsal spine in *Balistes* (2-13 per cent SL) was generally longer than in *Melichthys* and *Xanthich-*

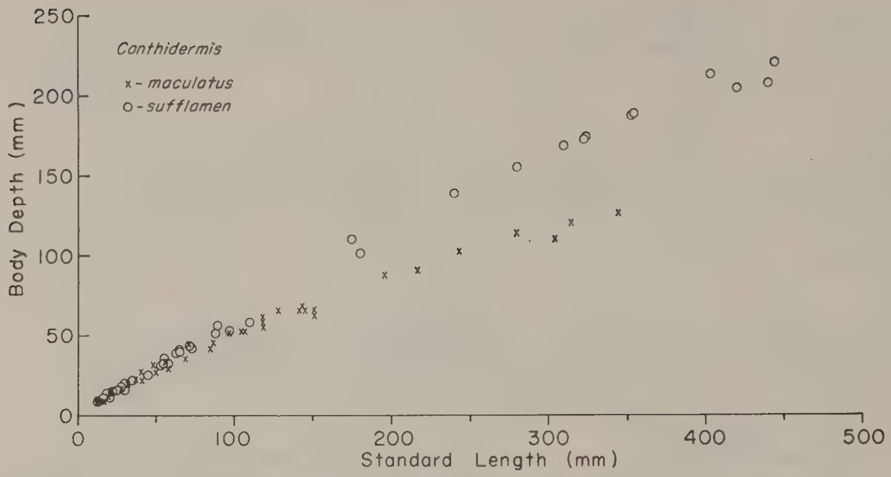

FIGURE 9. Relation of body depth to standard length for *Canthidermis maculatus* and *C. sufflamen* from the western Atlantic.

thys (0-2 per cent SL) in all sizes examined. The length of the third dorsal spine in the two species of *Canthidermis* (0-8 per cent SL) varied too greatly to be diagnostic.

LENGTH OF THE LONGEST DORSAL SOFT RAY: This length is the distance from the insertion to the tip of the longest dorsal soft ray, measured along the side of the ray. On specimens which are larger than 150 mm SL, as shown in Figure 8, the longest dorsal rays in *B. vetula* (36-71 per cent SL) are usually longer than those in *B. capriscus* (23-29 per cent SL). This is true also for *B. vetula* in comparison with *Canthidermis* (22-36 per cent SL), and *M. niger* (16-22 per cent SL). *M. niger* is separable from the longer-rayed *B. capriscus*. On specimens smaller than 100 mm SL, the longest dorsal rays of all six species are generally short. They are about equal to, or slightly shorter than, those on large specimens of *C. maculatus*, *B. capriscus*, and *M. niger*.

LENGTH OF LONGEST ANAL SOFT RAY: This length is the distance from the insertion to the tip of the longest anal soft ray, measured along the side of the ray. The longest anal soft ray in *C. sufflamen*, *C. maculatus*, *B. vetula*, and *B. capriscus* (20-35 per cent SL) is longer than in *X. ringens* (16-19 per cent SL) on specimens larger than 100 mm SL, and longer than in *M. niger* on specimens over 200 mm SL (16-19 per cent SL).

BODY DEPTH: The body depth is the vertical distance from the point of emergence of the pelvic process to the base of the first dorsal fin. In *C.*

maculatus and *X. ringens*, body depth decreases greatly in proportion to standard length in larger specimens (Figs. 4, 5), whereas in the other four species there is little or no decrease (Figs. 1, 2, 3, & 6). In specimens larger than 150 mm SL, *C. maculatus* (36-45 per cent SL) is separable from *C. sufflamen*, *Balistes*, and *Melichthys* (47-63 per cent SL) by means of this character. Figure 9 gives a comparison between *C. maculatus* and *C. sufflamen*. For small specimens in the range of 10-50 mm SL, body depth as a percentage of standard length is generally great (48-77 per cent SL) for all of the species examined (Figs. 2C, 5C, & 6C); it is usually as great as in large specimens of *Balistes* and *C. sufflamen* (Figs. 1A, 2A, & 6A). Another body depth, the distance between the origins of the second dorsal fin and anal fin, was also measured, but the differences among species, though similar to those for the depth measurement discussed above, were less distinct.

DEPTH AT CAUDAL PEDUNCLE: This measurement is defined as the least vertical depth. The depth at the peduncle is generally greatest in *Canthidermis* (Figs. 5 & 6). When specimens larger than 50 mm SL are considered, the two species of *Canthidermis* have a deeper caudal peduncle (10-15 per cent SL) than either *B. vetula* (7-9 per cent SL) or *X. ringens* (7-8 per cent SL). On specimens larger than 100 mm SL, the peduncle in the two species of *Canthidermis* is usually deeper (10-14 per cent SL) than in the other four species (7-10 per cent SL).

Fifteen other body parts were measured (fork length; total length; head length; postorbital head length; snout width; distances of snout to second dorsal fin, to anal fin, to pectoral fin, and to pelvic process; caudal peduncle length; lengths of second dorsal-fin base and anal-fin base; lengths of first and second dorsal spines; and pectoral-fin length). None proved useful for separating species. For most sizes examined, measurements for some body parts are proportionately similar in all of the species; for other body parts the range within a species is wide.

RANGES OF SPECIES

All six species occur in tropical waters; two have circumtropical distributions.

B. capriscus is known to occur in the eastern and western tropical Atlantic. Its range in the western Atlantic extends from Nova Scotia through the Gulf of Mexico to Argentina (Briggs, 1958: 298).

B. vetula has been recorded from the Indian Ocean, the western Pacific, and the eastern and western tropical Atlantic; it has a known range in the western Atlantic from Massachusetts through the Gulf of Mexico to Brazil (Briggs, 1958: 298; de Beaufort, 1962: 282).

M. niger has a circumtropical distribution and is usually associated with coral reefs. In the western Atlantic, its range is from Bermuda, Bahamas, south Florida, and Texas[3] to Brazil (Briggs, 1958: 299; de Beaufort, 1962: 284).

X. ringens is known only from the western Atlantic, from Bermuda and South Carolina through the northern Gulf of Mexico and to the Lesser Antilles (Briggs, 1958: 299; excluding reference to Indian Ocean).

C. maculatus is circumtropical; its range in the western Atlantic is from New Jersey through the northeastern and southeastern Gulf of Mexico to Argentina.[4]

C. sufflamen has been recorded only in the western Atlantic, from Massachusetts to Bermuda, through the Gulf of Mexico, to the Lesser Antilles (Briggs, 1958: 298).

SPECIMENS EXAMINED

The specimens are listed below by species and arranged by location of capture, generally from north to south. Specimens listed without a designation of museum or collection are in the collections of the U. S. Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida (TABL).

The following abbreviations are used:

ANSP	Academy of Natural Sciences of Philadelphia
BLBG	U. S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia
BLGT	U. S. Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas
BU	Boston University
ChM	Charleston Museum, South Carolina
CNHM	Chicago Natural History Museum
MCZ	Museum of Comparative Zoology, Harvard
SIO	Scripps Institution of Oceanography
SU	Stanford University
TU	Tulane University
UCLA	University of California at Los Angeles
UF	University of Florida
UMML	University of Miami Marine Laboratory
UMMZ	University of Michigan Museum of Zoology
USNM	U. S. National Museum
Cr.	cruise
Reg.	regular station
Spc.	special station
Std.	standard station
Sta.	station
Supl.	supplementary station

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[3] The known range is extended to Texas since several live specimens, which I later examined, were captured on a reef off Galveston (28°10′N., 94°18′W.) in October, 1965, by personnel of Sea Arama of Texas, Galveston.

[4] The known range is extended north to New Jersey and south to Argentina by respectively listing the following specimens of *C. maculatus*: Boston University, uncatalogued, collected on a cruise of the DELAWARE at 39°44′N., 77°00′ W., 59.4 mm SL; and Museum of Comparative Zoology, Harvard, MCZ 11887, collected at Buenos Aires, 151 mm SL.

Balistes capriscus.—Newport, R. I., (1 specimen) 66.8 mm SL, ANSP 804. SILVER BAY Sta. 1271, (1) 73.5. GILL Cr. 3, Reg. 64, (1) 55. GILL Cr. 3, Reg. 63, (2) 70-72. SILVER BAY Sta. 3348, (2) 218-319. GILL Cr. 8, Reg. 55, (1) 60. SILVER BAY Sta. 3330, (1) 231. SILVER BAY Sta. 2525, (1) 116. GILL Cr. 3, Reg. 61, (2) 19-50. SILVER BAY Sta. 3324, (4) 215-309. GILL Cr. 3, Reg. 62, (3) 15-64.5. GILL Cr. 4, Reg. 32, (1) 18.5. 16 miles south of Horn Island Pass, Mississippi, 26-27 Jan. 1959, (2) 103-127. SILVER BAY Sta. 4344, (4) 20.5-81.4. SILVER BAY Sta. 3757, (1) 255. GILL Cr. 8, Reg. 18, (1) 27. COMBAT Sta. 474, (14) 24-75. SILVER BAY Sta. 923, (1) 115. GUS Cr. 2, Sta. E 26, (1) 118.5, BLGT. GILL Cr. 4, Reg. 15, (1) 23. GILL Cr. 4, Reg. 16, (1) 30. OREGON Sta. 1372, (2) 14.8-15.6. OREGON Sta. 1356, (4) 22.6-53.2. GUS Cr. MWT 1, Sta. 1-3, 19 Sept. 1963, (1) 207, BLGT. BELLE OF TEXAS Cr. 28, Sta. E 11, (1) 80.4, BLGT. MISS ANGELA Cr. 16, Sta. E 2, (3) 94.5-108.5, BLGT. BELLE OF TEXAS Cr. 28, Sta. E 2, (1) 157, BLGT. GUS Cr. 2, Sta. E 2, (1) 94.5, BLGT. BELLE OF TEXAS Cr. 30, Sta. E 2, (1) 91, BLGT. GUS Cr. 2, Sta. E 23, (1) 74.1, BLGT. BELLE OF TEXAS Cr. 28, Sta. E 15, (1) 81.3, BLGT. GUS Cr. 1, Sta. E 50, (1) 90.5, BLGT. OREGON Sta. 1134, (2) 13.1-16.9, CNHM 64243. GUS Cr. 10, Sta. W 24, (1) 176, BLGT. BELLE OF TEXAS Cr. 29, Sta. W 20, (1) 88.9, BLGT. COMBAT Sta. 459, (11) 17.5-67, BLBG. GUS Cr. 3, Sta. W 62, (1) 155, BLGT. COMBAT Sta. 458, (1) 20.6. Dade County, Florida, 1964, (1) 142.5, BLGT. Bear Cut in front of Marine Laboratory, Virginia Key, Dade County, Florida, (1) 27.2, UMML Supl. 220. 10 miles east of Sea Buoy, Miami, Florida, (2) 21.7-34.1, UMML Supl. 158. Jupiter Inlet, Palm Beach County, Florida, (1) 35, UF, BLBG. 10 miles east of Fowey Rocks Light, Florida, (1) 14.7, UMML NG31. 10 miles east of Fowey Rocks Light, Florida, (1) 21.3, UMML NG30D. Hawk Channel, Florida, (1) 146.5, UMML 6985. Off Matecumbe, Florida, (1) 13.8, UMML. 70 miles NW of Key West, Florida, (1) 107.5, UMML 1811. Dry Tortugas, Florida, (2) 88.8-189, UMML 1618. COMBAT Sta. 436, (1) 54. St. Martin Island, West Indies, (1) 44, ANSP 781. West Indies, (1) 23, MCZ 11875. Old Providence Island, western Caribbean, (2) 22.8-24, ANSP 72750.

Balistes vetula.—Twenty miles south of Aransas Pass, Texas, (1) 387, BLGT. South Lake Worth, Palm Beach, Florida, (1) 45, UF 4077. Crandon Park Marina, Key Biscayne, Florida, (1) 16.4, UMML Supl. 221. Bimini, Bahamas, (1) 196.5, UMML 7943. SILVER BAY Sta. 3479, (2) 176-261, BLBG. Nassau, Bahamas, (1) 158.5, USNM 53241. SILVER BAY Sta. 3493, (1) 292. Pigeon Cays, 11 miles SE of Andros Island, Bahamas, (1) 271.5, UMML 1789. Bahamas, (3) 188-202, USNM 6103. Puerto Rico, (1) 178.5, USNM 126421, FISH HAWK. Jamaica, (1) 140, USNM 160723. Ambergris Cay, Yucatán, Mexico, (1) 93, USNM 79248.

Calvary Bay, St. John, Virgin Islands, (1) 133, UMML 6660, V.I. Sta. 12. OREGON Sta. 3563, (2) 225-274. Marigot Lagoon, St. Lucia, BWI, (2) 40.6-44.4, USNM 170139. Between Main Island and Pigeon Island, St. Lucia, BWI, (1) 49.5, USNM 170212. Kingston, St. Vincent Island, BWI, (1) 53.5, ANSP 39846. Old Providence Island, western Caribbean, (5) 33.2-36.1, ANSP 72750. Tobago Cays, Grenadines, (2) 39-55.5, USNM 170174. No data, (1) 250, UMML.

Balistes polylepis.—PACIFIC: Magdalena Bay, north end of Sta. Margarita Island, Baja California, Mexico, (1) 288, SIO 60-355-34A. Off Isla Nayarit, Isabella, Mexico, (1) 295, SIO 62-65-34A. Panamá—purchased, (2) 76.8-80.0, ANSP 45131-32.

Balistes punctatus.—Porto Grande, St. Vincent, Cape Verde Islands, (1) 342, USNM 42173. Off mouth of St. Paul River, Liberia, (1) 193, USNM 197498. Mensurado River Beach, Liberia, (1) 202, USNM 197497. Market at Lagos, Nigeria, (1) 63.3, ANSP 101327. Mbode, Cameroon, Africa, (2) 133-134, SU 15949.

Melichthys niger.—Outer reefs, Bermuda, (1) 163, USNM 175778. Dade County, Florida, (1) 240, BLGT. Bimini, Bahamas, (1) 223, UMML 7944. Hogsty Reef, NW Cay, Bahamas, (1) 282, ANSP Chaplin Bahamas Collection, Sta. 578. Hogsty Reef, NW Cay, Bahamas, (1) 246, ANSP Chaplin Bahamas Collection, Sta. 581. Hogsty Reef, NW Cay, Bahamas, (3) 251-292, ANSP Chaplin Bahamas Collection, Sta. 585. Rum Cay, Bahamas, (1) 270, USNM 38372. Cuba, (1) 262, USNM 25238. Tropical Research Medical Laboratory, San Juan, Puerto Rico, (2) 222-230, UMMZ 172720. Tropical Research Medical Laboratory, San Juan, Puerto Rico, (1) 211, UMMZ 172734. La Parguera, Puerto Rico, (1) 96, UMMZ 673096. Congrejos, Puerto Rico, (1) 150, UMML 2168. St. Andrews Cay, Caribbean Sea, (1) 249, ANSP 89029. OREGON Sta. 4987, (1) 93.5. Pelican Island, Barbados, BWI, (1) 115, SU 37293. Ascension Island, (1) 254, USNM 42308. Ascension Island, (3) 179-188, BU, uncatalogued CRAWFORD Cr. 10.

PACIFIC: Revillagigedos Islands, Clarion Islands, (1) 305, UCLA W53-52. Clipperton Island, (8) 126-265, UCLA W56236. Isla de Cocos, Costa Rica, (1) 113, UCLA W53-126. Isla de Cocos, Costa Rica, (2) 205-207, SIO 59-334-34A.

Xanthichthys ringens.—Bermuda, (1) 74, USNM 178037. GILL Cr. 3, Spc. 5, (1) 47.7. SILVER BAY Sta. 4369, (1) 39.6. OREGON Sta. 1356, (1) 31.7. OREGON Sta. 1380, (2) 18.1-39.5, UMML 2975. SILVER BAY Sta. 4371, (2) 23.8-43.4. SILVER BAY Sta. 4373, (1) 47. GILL Cr. 3, Std., 26°23′N, 76°46′W, (2) 40.7-46.1. GILL Cr. 7, Std., 26°20′N, 76°47′W, (2) 36.4-49.1. GILL Cr. 7, Std., 26°20′N, 76°44′W, (2) 37.4-49.6, BLBG. GILL Cr. 3, Std., 26°20′N, 76°43′W, (1) 65.3. GILL Cr. 3, Std., 26°19′N, 76°45′W, (1) 38. Grand Bahama Island, (1) 90, ANSP Sta. 61-F. Havana, Cuba, (1) 150, USNM 24792. Havana, Cuba, (2) 151-163.5, ANSP 87891. Cozumel Island, Yucatán, Mexico, (1) 160.5, UMML 9414. OREGON Sta. 1294, (2) 28.0-50.6. Four miles SE of Rams Head, St. Johns, Virgin Islands, (2) 97.5-100.5, UMML 6249, V.I. Sta. 112. Port Castries, St. Lucia, BWI, (1) 119, ANSP 74895. Courtown Cay, western Caribbean, (1) 28.4, ANSP 72782. No data, (1) 161, USNM 9481.

Xanthichthys mento.—PACIFIC: Near Melponone Cove, Guadalupe Island, Baja California, Mexico, (1) 229, SIO H53-173. San Benedicto, Bahía, Revillagigedos Islands, Mexico, (2) 216-224, UCLA, W-55-150. Socorro Island, Revillagigedos Islands, Mexico, (4) 210-227, UCLA W51-92. Anchorage in Bahia, Socorro Island, Revillagigedos Islands, Mexico, (3) 200-209, UCLA W-55-123. Bahía, Clarion Island, Revillagigedos Islands, Mexico, (1) 212, SIO 57-138-34B.

Canthidermis maculatus.—39°44′N, 70°00′W, (1) 59.4, BU, DELAWARE. 36°57′N, 68°05′W, (1) 36.8, BU, uncatalogued, DELAWARE. Flatts Inlet, Bermuda, (2) 14-17.7, CNHM 48623. Argus Bank, Bermuda, (1) 86.9, CNHM 48578. Argus Bank, Bermuda, (1) 143, UMMZ 176500. Seabrooks Beach, South Carolina, (1) 244, ChM 34.360. Gulf Stream, (1) 129, MCZ 11901. 31°03′N, 45°58′W, (1) 196, MCZ 39769. COMBAT Sta. 474, (1) 69.4. SILVER BAY Sta. 4369, (1) 72. Gulf of Mexico, halfway between shore and Continental slope, (1) 345, USNM 158569. OREGON Sta. 1590, (1) 109, UF 3194. OREGON Sta. 820, (2) 130-151, TU 6732. OREGON Sta. 1616, (1) 107, ANSP Tyler Collection. Florida Current, (1) 41, UMML 4433, Supl. 27. Crandon Park Marina, Key Biscayne, Florida, (1) 15.8, UMML, 8 Feb., 1961. Miami, Florida, Pier 5, (1) 105.5, UMML 431. Off Miami, Florida, (1) 280, UMML 10933. Terminal Yacht Basin, Miami Beach Causeway, Dade County, Florida, (1) 49.0, UMML 2556. Biscayne Bay at Pier 5, Dade County, Florida, (1) 304.5, UMML 9317. Miami, Coconut Grove, Biscayne Bay, Dade County, Florida, (3) 13.5-21.7, UMML 3976. Bimini, Bahamas, (1) 142, ANSP 67717. COMBAT Sta. 457, (2) 57.8-85.0, BLBG. OREGON Sta. 2196, (1) 315. OREGON Sta. 1068, (1) 217, ANSP Tyler Collection. OREGON Sta. 1234, (1) 40.3, CNHM 61360. 19°40′N, 74°30′W, (1) 145, BU, ATLANTIS. ATLANTIS Sta. 5581, 19°12′N, 62°05′W, (1) 37.1, BU. West Indies, (1) 119, MCZ 11875. Buenos Aires, (1) 151, MCZ 11887. No data, (1) 119, MCZ 39766.

PACIFIC: Salina Cruz, Bahía, Chipequa, Mexico, (1) 212, SIO 58-375. 150 miles SW of Acapulco, Mexico, (1) 154, SIO 62-168-34B. 100 miles in Pacific, between Guatemala and El Salvador, (1) 228, SIO 57-75. 0-1 mile NW of wreck on NE shore of Clipperton Island, (3) 415-475, UCLA

W56236. 14°01′N, 116°13′W, (1) 210, SIO 58-370. 10°00′N, 111°08′W, (1) 236, SIO 55-227. 08°00′N, 115°37′W, (2) 211-227, SIO 58-368. 05°00′N, 78°09′W, (1) 235, SIO 55-245. 04°53′N, 81°30′W, (3) 51.9-78.5, ANSP 86765. 04°03′N, 78°47′W, (1) 211, SIO 55-243.

Canthidermis sufflamen.—38°08′N, 70°58′W, (1) 74.9, CNHM, Bear. 38°05′N, 65°58′W, (1) 180, BU, Delaware. 36°42′N, 70°00′W, (1) 38.7, BU, Delaware, 3 Oct., 1957. Silver Bay Sta. 2172, (1) 23.3. Gill Cr. 8, Reg. 80, (1) 34.8. Silver Bay Sta. 2201, (1) 24.0. Gill Cr. 7, Reg. 73, (1) 50.3. Flatts Inlet, Bermuda, (3) 12.6-15.0, CNHM 48623. Gill Cr. 7, Reg. 72, (1) 30.0. Gill Cr. 2, Reg. 59, (1) 12.6. Gill Cr. 2, Reg. 40, (1) 15.5. Gill Cr. 3, Reg. 26, (1) 88.5. Gill Cr. 8, Reg. 18, (2) 11.8-19.8, BLBG. Combat Sta. 474, (2) 35.3-58.1. Silver Bay Sta. 471, (1) 30.2. Gill Cr. 7, Reg. 17, (1) 27.2. Combat Sta. 315, (2) 21.6-23.0. Oregon Sta. 638, (1) 92, TU 12748. Silver Bay Sta. 4369, (1) 55.7. Gill Cr. 3, Spc. 6, (1) 89. Oregon Sta. 1585, (1) 97.5, UF 1273. Gill Cr. 3, Reg. 8, (2) 13.3-18.7. Oregon Sta. 593, (1) 55.9, CNHM 59850. Silver Bay Sta. 4231, (1) 240. Silver Bay Sta. 4373, (1) 65.1. Silver Bay Sta. 4372, (1) 71.7, BLBG. Bear Cut in front of Marine Laboratory, Virginia Key, Biscayne Bay, Florida, (2) 21.7-22.8, UMML Supl. 220. Crandon Park Marina, Key Biscayne, Florida, (1) 12.0, UMML. Crandon Park Marina, Key Biscayne, Florida, (1) 12.6, UMML Supl. 221. Bear Cut, Dade County, Florida, (1) 280, UMML 5183. Off Florida, (1) 175, Marine Studios, Marineland, Florida. Bahamas, (1) 445, ANSP Chaplin Bahamas Collection Sta. 517. Off Lerner Dock, Bimini, Bahamas, (1) 324, UMML 1787. Hogsty Reef, West end of Northwest Key, Bahamas, (1) 353, ANSP Chaplin Bahamas Collection Sta. 585. Yacht Basin, Pier 5, Miami, Florida, (1) 26.2, UMML 785. Bimini and/or Cat Key, Bahamas, (4) 12.4-17.4, UMML 1464. One mile off Brackens Hotel, Palm Beach, Florida, (1) 376, CNHM 46789. Jupiter Inlet, Palm Beach County, Florida, Aug., 1958, (1) 56, UF. Combat Sta. 459, (1) 33.6. Oregon Sta. 1035, (1) 49, TU 10935. Oregon Sta. 1298, (1) 96.5, BLGT. Gill Cr. 3, Std. 26°23′N, 76°50′W, (1) 109.5. Gill Cr. 7, Std. 26°20′N, 76°44′W, (1) 54.1. Gill Cr. 7, 26°06′N, 78°08′W, (1) 32.2. Oregon Sta., 25°N, 89°W, Gulf of Mexico, (1) 44.9, CNHM 46693. Combat Sta. 436, (1) 53.1. Yucatán, Mexico, (2) 421-441, USNM 157714. Off La Parguera, Puerto Rico (1) 63, UMML 5888. La Parguera, Puerto Rico, (1) 310, UMML 2422. St. Johns, Virgin Islands, (1) 404, UMML 5147, V.I. Sta. 24. St. Martin Island, West Indies, (1) 65.2, ANSP 800. St. Martin Island, West Indies, (1) 277, ANSP 806 (Skin). Oregon Sta. 3563, (1) 355. Santa Cruz, Curaçao, (1) 323, BLGT.

SUMARIO

PECES DE LA FAMILIA BALISTIDAE DEL ATLANTICO OCCIDENTAL

Seis especies de la familia Balistidae viven en el Atlántico Occidental: *Balistes capriscus, B. vetula, Melichthys niger, Xanthichthys ringens, Canthidermis maculatus* y *C. sufflamen.*

Se sitúa a *Melichthys piceus* en la sinonimia de *M. niger* y a *Canthidermis sobaco* en la sinonimia de *C. sufflamen.*

La pigmentación y coloración de las seis especies varía en los distintos ejemplares y en los mismos hay cambios marcados durante su desarrollo.

Tres especies: *Balistes capriscus, B. vetula* y *Melichthys niger* tienen escamas o placas de mayor tamaño inmediatamente posterior a la abertura de las branquias y también una articulación flexible conectando la parte externa expuesta del proceso pelviano con la parte proximal del proceso que descansa bajo la piel. Las otras tres especies carecen de estos caracteres. Las tres primeras especies difieren en el número de radios anales (*B. capriscus,* 23-26 radios anales; *B. vetula,* 27-28; *M. niger,* 29-31). Las otras tres especies también difieren entre sí en el número de radios de algunas de sus aletas. *C. maculatus* tiene menos radios anales (menos de 23) que *C. sufflamen* y *X. ringens*; y *C. sufflamen* tiene más radios pectorales (más de 14) que *X. ringens.*

Los cachetes de *X. ringens* tienen escamas alargadas verticalmente, separadas por tres surcos laterales. Los lados de *M. niger* tienen de 8 a 11 hileras horizontales de escamas con crestas que tienen espinas dirigidas anteriormente.

La distancia del ojo a la primera espina dorsal es mayor en *Canthidermis* (mayor que el 11 por ciento de la longitud media en ejemplares mayores de 50 mm de longitud media) que en los otros tres géneros. En ejemplares de más de 150 mm de longitud media los radios dorsales más largos son más largos en *B. vetula* (más del 29 por ciento de la longitud media) que en *B. capriscus* y el cuerpo de *C. sufflamen* es más alto (mayor del 45 por ciento de la longitud media) que el de *C. maculatus.*

Las seis especies viven en aguas tropicales; dos, *M. niger* y *C. maculatus,* tienen distribución circuntropical. Se extiende la distribución de dos especies en el Atlántico Occidental: *M. niger* hasta Texas y *C. maculatus* hasta New Jersey y la Argentina.

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Reproduction and Development of *Sebastodes paucispinis* and Comparison with Other Rockfishes off Southern California

H. Geoffrey Moser

The elongate paired testes of *Sebastodes paucispinis* consist of numerous tubules radiating from a single sperm duct that extends along the surface of each testis. The paired sperm ducts converge at the posterior ends of the testes to form a single median duct which continues into the urogenital papilla, a probable intromittent organ. The ovaries are paired fusiform structures consisting of dense stroma and ovigerous tissue surrounded by a thin-walled muscular sac that also serves as a gonoduct. These ducts unite posterior to the ovaries to form a duct which exits between the anus and the urinary papilla. An unusual vascular system insures that the gonads receive a large and even supply of arterial blood.

The testes of *S. paucispinis* are small during the early stages of spermatogenesis which take place from January to May. During the final stages of spermatogenesis (June–September) the testes enlarge and become pale white. Spermatogenesis terminates in September at which time the mating period probably begins. The ovaries undergo greater seasonal changes than the testes. Ovaries are small during the post-extrusion period from March to June. Vitellogenesis, which begins in July and continues throughout the summer, causes the ovaries to enlarge and become opaque yellow. The first pregnant females appear in October. In early gestation ovaries are translucent yellow but gradually they become darker as the embryos develop melanistic pigment. Females begin to give birth to their first brood in November. Maturation, fertilization, and development of a second brood follows immediately. Most females have gestated and released their second brood by March.

The embryonic stages of *S. paucispinis* are similar to those of oviparous marine teleosts and specialized structures for nutritional and respiratory exchange are not developed. Gestation lasts about one month and the young are born as hatched, yolkless larvae, 4–6 mm long, with well-developed eyes, jaws, and pectoral fins. The larvae occupy the upper mixed layer and have a wide geographical distribution. They transform into juveniles at about 30 mm SL and move into shallow waters (usually less than 20 m) where they spend their first year.

The gonad cycles of other species of *Sebastodes* are similar to that of *S. paucispinis*. Although most of the species examined gestate and give birth to young during the winter off southern California, species of one group (*S. rosaceus* and relatives) gestate and extrude young during the spring and summer. The early larval stages of 15 other species of *Sebastodes* are illustrated and compared with those of *S. paucispinis*.

Introduction

MORE than 50 species of rockfishes, included within the genus *Sebastodes*, inhabit California waters. Early workers (*e.g.*, Jordan, 1884; Eigenmann, 1892, 1894) found that all the members of this genus are livebearers and produce large numbers of young. A number of investigators (Smith, 1936; Wales, 1952; Westrheim, 1958; Alverson and Westrheim, 1961; Clemens and Wilby, 1961; Hitz, 1962; DeLacy, Hitz, and Dryfoos, 1964; Phillips, 1964; John S. MacGregor, MS.) have reported on the fecundity and seasons of gestation of rockfishes inhabiting the coasts of California, Oregon, Washington, and British Columbia. Their reports indicated that each species has a well-defined season of gestation. Also, they corroborated the high fecundity estimates of early workers and, in general, showed that fecundity is related to the size of the species. For example, Phillips (1964) found 6200–50,000 maturing ova in a series of *Sebastodes jordani*, a small rockfish, and 20,000–2,297,000 maturing ova in a series of *Sebastodes paucispinis*, a large rockfish.

The literature contains little information on rockfish development. Eigenmann (1892) described intra-ovarian stages of *S. rubrivinctus*. He found that the young of this species are hatched within the ovary after a one-month gestation period and are extruded as 5-mm larvae. Wales (1952) described the embryos of *S. mystinus*. Morris (1956) attempted to rear larvae extruded from females of *S. paucispinis*, *S. goodei*, *S. jordani*, and *S. saxicola*. His descriptions of the early post-extrusion larvae of these species were the first presented for the genus *Sebastodes*. DeLacy, Hitz, and Dryfoos (1964) described the gross seasonal changes in the ovaries of *S. auriculatus* and *S. caurinus* and illustrated the pre-extrusion larvae of nine species of rockfish.

The larvae of *Sebastodes* are planktonic. Since 1949, the plankton studies of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) have accumulated data on the distribution and abundance of these larval stages (Ahlstrom, 1961). *Sebastodes* larvae are wide-ranging within the area encompassed by the CalCOFI survey. At some latitudes larvae are found over 400 miles from the coast. *Sebastodes* larvae are most abundant in plankton tows taken during the winter and spring (December–April). The larvae have a restricted vertical distribution centered within or above the thermocline (Ahlstrom, 1959). All of these investigations have treated rockfish larvae at the generic level and no attempt has been made to define the distribution and abundance of separate species.

A description of the male and female reproductive systems of *S. paucispinis* Ayres is presented here. The extraordinary gonadal vascular system of rockfish was first described by Allen (1905) in a survey of the vascular anatomy of cottoid fishes. A description of the vascular system in *S. paucispinis* is included here because the system in *S. paucispinis* differs slightly from those of the six species examined by Allen, and sexual dimorphism of the vascular system, found in *S. paucispinis*, was not treated by Allen. Monthly collections of *S. paucispinis* during 1964 provided an opportunity to study the seasonal changes in the testes and ovaries. Comparative observations on gonadal changes in other rockfish species are also given. The first complete series of life history stages for a species of rockfish, *S. paucispinis*, is given in this paper along with data on the horizontal distribution of larvae and the vertical distribution of juveniles and adults. In addition, the early larval stages of 15 other species are described and illustrated.

MATERIALS AND METHODS

During the investigation, 1611 urogenital tracts were collected from 30 species of rockfish. *S. paucispinis* was represented in 36 of the 51 collections made from January 1963 to July 1965. This species was collected in May, August, and December 1963, in all months except April during 1964, and in January and July of 1965, thus providing data on three annual reproductive cycles.

Two principal methods of collection were employed. Adult rockfish were collected by hook and line on cruises of the R/V BLACK DOUGLAS (U. S. Bureau of Commercial Fisheries) and the R/V VELERO IV (University of Southern California), primarily from Cortes, Tanner, and Forty-three Fathom banks, off San Diego, California. The standard length of each fish was recorded and the urogenital system was removed and preserved in 10% formalin.

The other principal source of material was the "set line" fishery at Newport Beach, California. Specimens obtained here were usually fresh since the fish arrived at the market within one to several hr after they were caught. Several of the fisherman fished exclusively for *Sebastodes*, especially *S. paucispinis*, making the fishery an invaluable source of material.

Materials for the life history studies were gathered from various sources. Developmental stages up to the early larval stages were collected from pregnant females. Later larval stages of *S. paucispinis* were obtained from the CalCOFI plankton collections. Juveniles collected by bottom trawl, seine, hook and line, or poisoning were loaned by: Dr. Richard H. Rosenblatt of Scripps Institution of Oceanography; Mr. John E. Fitch and Mr. Julius B. Phillips of the California Department of Fish and Game; Mr. Wayne Baldwin of the University of California, Los

Angeles; and Dr. John R. Hunter of the Bureau of Commercial Fisheries.

The urogenital system of each specimen was examined with a stereoscopic microscope and the right gonad of each excised, blotted with a paper towel to remove excess water, and weighed to 0.01 g. The "gonad index" was calculated for each specimen according to the formula, [gonad weight/(standard length)^3] × 10^7, modified from Shiokawa (1962). The gonad weight, the gonad index, and the measurements of the urogenital system are listed for individual specimens (Moser, 1966). Diameters of ova and embryos were measured with the ocular micrometer of a stereoscopic microscope. DeLacy, Dryfoos, and Hitz (1964) demonstrated that rockfish ovaries have a residual supply of unyolked ova which are less than 0.2 mm in diameter and that a series of maturing ova enlarge synchronously in each ovary before the gestation season. Thus, for the present investigation only maturing ova or developing embryos were measured. A few ova were selected randomly for measurement from each female. If a brood of embryos was also present, the long axes of several embryos were also measured. Median diameters of the ova and lengths of the embryos were obtained for each specimen.

For the morphological study of the urogenital vascular system of *S. paucispinis*, pigmented fluid latex was injected into about two dozen fresh specimens. Latex was introduced into the arterial system through one of the efferent branchial arteries. The venous system was injected with latex of a different color through the caudal vein. The hardening of the latex with fixation in 10% formalin allowed observation and manipulation of the most delicate vascular elements.

Whenever possible, living embryos or larvae were extruded from pregnant females into jars of sea water and kept alive in a shipboard refrigerator where they continued to develop. In the shoreside laboratory the young were incubated at a series of temperatures in a temperature gradient block until all yolk was utilized. This technique provided specimens for life history description as well as information on the sequence and rate of pigment formation and the rate of yolk utilization. Respiration rates of embryos were studied with a Warburg respirometer and standard manometric techniques.

In this paper the body length of a larva, prior to caudal fin formation, is measured from the anterior edge of the snout to the posterior tip of the notochord. In *S. paucispinis* the caudal fin is formed at about 9 mm and thereafter the body length (standard length) is measured from the anterior edge of the snout to the posterior margin of the hypural plate.

Morphology of the Testes in *S. paucispinis*

The testes of *S. paucispinis* are elongate paired organs, of about equal size, located in the posterior region of the peritoneal cavity, midway between the dorsal and ventral boundaries of the cavity (Fig. 1). The testes are contiguous at their posterior ends but gradually diverge anteriad. Each is supported by a mesorchium that extends from the ventro-lateral border of the gas bladder and attaches to the testis along its dorsal surface. Posterior to the gas bladder the mesorchia unite with the single median fold which supports the urinary bladder. Cross sections of the testes are generally triangular except at their anterior and posterior ends where the cross sections are elliptical to round.

A sperm duct (Fig. 1) lies in a dorsal groove along each testis. Anteriorly each duct is embedded below the surface of the testis, but posteriorly it becomes larger and more superficial. The paired ducts emerge from the posterior ends of the testes and unite to form a single median sperm duct. This duct courses posteriad between the urinary bladder and the intestine, then continues into the urogenital papilla (Fig. 1). It exits through a pore (Fig. 2A) just anterior to the urinary pore on the tip of the papilla. The elongate cylindrical papilla probably serves as the intromittent organ.

Arterial System.—Two arteries of equal size, the dorsal aorta and the coeliaco–mesenteric artery, are formed by the confluence of the paired efferent branchial arteries at the base of the first vertebra (Fig. 1A). The coeliaco–mesenteric artery courses posteriad a short distance and then divides into a dorsal branch, the mesenteric artery, and a ventral branch, the coeliac artery.

The mesenteric artery continues posteriad giving off a smaller branch, the left gastric artery, just anterior to the transverse septum. These two arteries penetrate the transverse septum directly dorsal to the esophagus, then immediately diverge laterally. The left

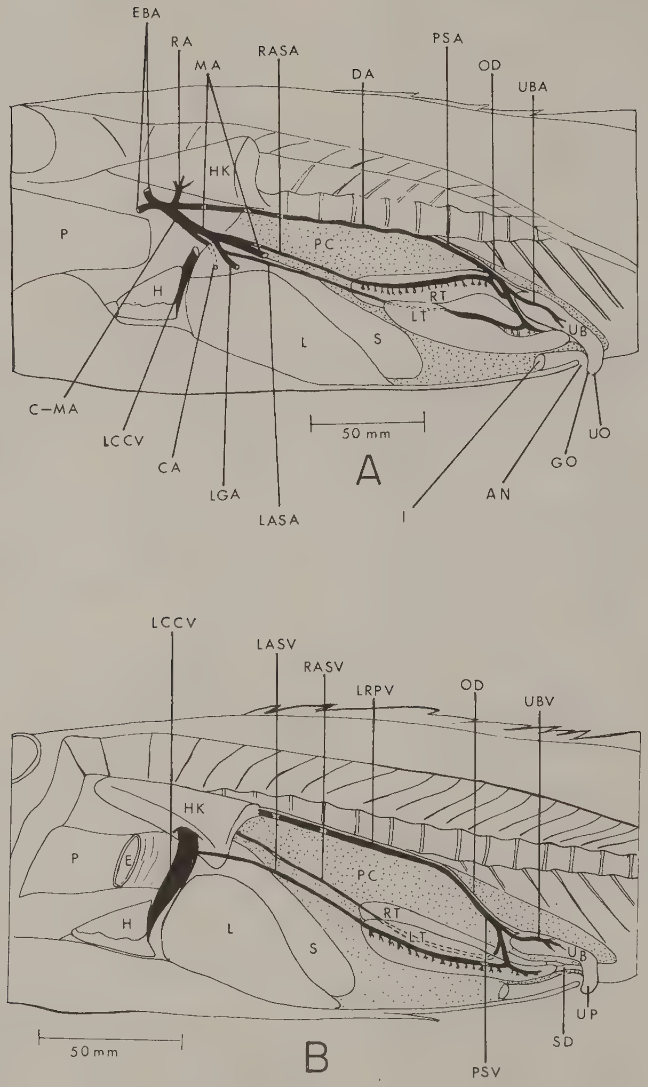
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Fig. 1. Ventrolateral view of male urogenital system of *Sebastodes paucispinis*. A. Arterial system of 473-mm SL specimen collected 6 August 1965. B. Venous system of 407-mm SL specimen collected 13 July 1965. AN, anus; CA, coeliac artery; C–MA, coeliaco–mesenteric artery; DA, dorsal aorta; E, esophagus; EBA, efferent branchial arteries; GO, genital opening; H, heart; HK, head kidney; I, intestine; L, liver; LASA, left anterior spermatic artery; LASV, left anterior spermatic vein; LCCV, left common cardinal vein; LGA, left gastric artery; LRPV, left renal portal vein; LT, left testis; MA, mesenteric artery; OD, opisthonephric duct; P, pharynx; PC, peritoneal cavity; PSA, posterior spermatic artery; PSV, posterior spermatic vein; RA, renal artery; RASA, right anterior spermatic artery; RASV, right anterior spermatic vein; RT, right testis; S, stomach; SD, sperm duct; UB, urinary bladder; UBA, urinary bladder artery; UBV, urinary bladder vein; UO, urinary opening; UP, urinary papilla.

gastric artery gives off a branch, the left anterior spermatic artery, which runs directly posteriad to the left testis. After penetrating the transverse septum the mesenteric artery courses posteriad within the dorsal mesentary along the right dorso-lateral border of the stomach. Posterior to the transverse septum it gives off a branch, the right anterior spermatic artery, which runs directly posteriad to the right testis. Both the right and left anterior spermatic arteries are supported by anterior extensions of the mesorchia.

The testes also receive arterial supply at their posterior ends. The dorsal aorta, after giving off the coeliaco–mesenteric artery and the renal arteries, continues posteriad in a shallow groove at the base of the vertebral column. At about the seventh vertebra the single posterior spermatic artery branches off, enters the peritoneal cavity, and proceeds ventro-posteriad within the connective-tissue sheath containing the paired opisthonephric ducts and the posterior spermatic vein. Upon reaching the anterior tip of the urinary bladder, the posterior spermatic artery gives off the urinary bladder artery, then turns ventrad and immediately divides into paired posterior spermatic arteries of equal size. As these arteries reach the testes, each gives off a small branch which turns posteriad along the dorso-medial surface of the testis. The posterior spermatic arteries then turn anteriad and traverse the dorsal surface of each testis. These arteries are continuous with the anterior spermatic arteries which originate from the mesenteric and left gastric arteries. Thus, blood is supplied to each testis by an "arterial loop," an effective mechanism for insuring even distribution of oxygen along the entire length of the testis.

In their paths along the dorso-medial borders of the testes, the spermatic arteries lie within the mesorchia. Each artery sends out numerous ventral branches along the entire length of the testis. After entering the fibrous capsule of the testis these ventral branches diverge transversely into small branches which supply the gonadal tissue.

Venous System.—The venous drainage of the urogenital system in *S. paucispinis* parallels the arterial supply (Fig. 1B). A spermatic vein runs along the dorso-medial border of each testis between the spermatic artery and the testis. It receives branches that drain the testis in a manner mirroring the arterial branches. Spermatic veins of small diameter depart from the anterior ends of the testes and proceed anteriad, adjacent to the anterior spermatic arteries. Near the transverse septum the anterior spermatic arteries and veins separate. The veins continue dorso-anteriad, penetrate the transverse septum at the lateral borders of the kidneys, and enter the medial surfaces of the left and right common cardinal veins, at a point immediately ventral to where the latter emerge from the head kidneys.

The diameter of the spermatic vein increases as the vein proceeds posteriad along the dorso-medial borders of each testis. At the anterior end of the urinary bladder, the veins turn dorsad after receiving a pair of smaller branches which drain the posterior end of each testis. The paired posterior spermatic veins then continue dorsad to the anterior tip of the urinary bladder, where they combine to form a single posterior spermatic vein. Just dorsal to this confluence, the urinary bladder vein joins the posterior spermatic vein. The single posterior spermatic vein then runs dorsad to the midline of the peritoneal cavity. The vein reaches the dorsal midline at the 10th or 11th vertebra and

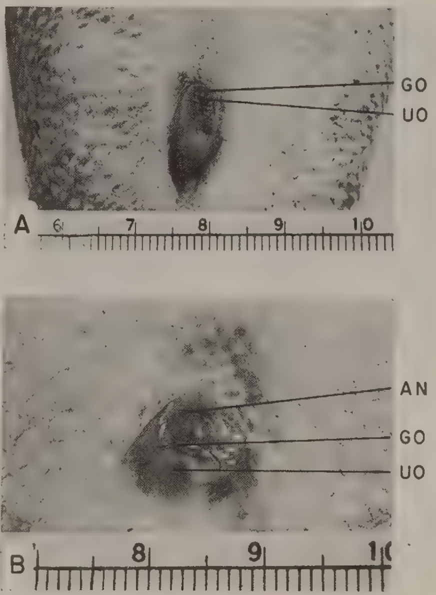

Fig. 2. Urogenital papilla of *Sebastodes paucispinis*. A. Adult male collected 6 August 1965. B. Adult female collected 6 August 1965. AN, anus; GO, genital opening; UO, urinary opening. (Scale in mm.)

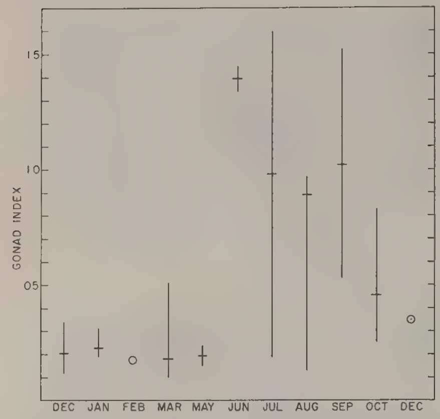

Fig. 3. Gonad indices of *Sebastodes paucispinis* males collected from Newport Beach, California, December 1963–December 1964. Vertical line indicates range of gonad indices and horizontal line indicates median gonad index for each month. Single records are circled. Gonad Index = [gonad weight/(standard length)^3] × 10^7.

enters the median renal portal vein. The renal portal vein divides into left and right renal portal veins just anterior to the point of entry of the posterior spermatic vein. The renal portal veins pass anteriad along the ventro-lateral borders of the vertebral column and enter the head kidneys where they form a capillary network. These capillaries then combine to form a short vein which joins with the anterior cardinal vein. The resultant common cardinal veins leave the lateral surface of each head kidney and run directly to the sinus venosus.

Thus, like the arterial supply, the venous drainage of the testis is a vascular loop. The anterior spermatic veins have very small diameters and the larger posterior spermatic veins are responsible for most of the venous drainage of the testes.

SEASONAL CHANGES IN THE TESTES OF *S. paucispinis*

Changes in Weight.—Changes in the weight and size of the testes during the year are less striking than those of the ovary, but they are clearly observable and reveal the cyclic nature of reproduction. Monthly changes in the relative weight of the testes, expressed as the gonad index, are shown in Fig. 3 for males collected at Newport Beach, California in 1964. Gonad indices were low during the initial stages of spermatogenesis from January to May. The marked increase in the weight and size of the testes in June, as shown by the high gonad indices for that month, reflected rapid cell proliferation during spermatogenesis. The gonad indices remained high from July through September as intense spermatogenesis continued. The gradual decrease in the gonad indices from October to December reflected the termination of spermatogenesis and the discharge of spermatozoa during mating.

Morphological Changes.—Testes collected from January to May have triangular cross sections with flat to concave sides (Figs. 4, 5). Two zones appear in these cross sections: (1) a triangular zone at the center consisting of efferent ductules radiating from the sperm duct and (2) an outer zone composed of tightly packed seminiferous tubules aligned perpendicularly to the border of the testis. Sperm, presumably left over from the previous mating season, appears in the sperm ducts at the posterior ends of the testes in some specimens, but by May no sperm is found, and the sperm ducts are collapsed. The testes are grayish to brownish and very tough and spongy at this time (Fig. 5C).

During the late stages of spermatogenesis, from July to September, cross sections of the testes appear homogenous, except for very small white areas scattered throughout. These white areas represent large cysts of spermatozoa. During this period spermatozoa begin to move centripetally from the seminiferous tubules and collect in the efferent ductules where they appear as silvery white clumps. At the posterior ends of each testis, the filling of the ductules with sperm gives the entire inner zone of the testis a silvery white appearance. Cross sections of the the testes appear rounded because of the swelling caused by cell proliferation. The testes are bright white during this period and are very fragile (Fig. 5A).

Spermatogenesis ceases in September. Spermatozoa continue to move inward from the seminiferous tubules and collect in the efferent ductules. The sperm ducts begin to fill with spermatozoa and each duct is visible as a rounded white longitudinal strip along the dorso-medial surface of each testis.

Sperm moves posteriad within the sperm duct and accumulates within the posterior region of the testis. The seminiferous tubules

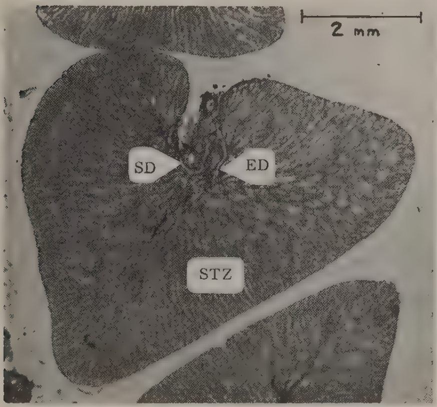

Fig. 4. Cross section of testis of 410-mm SL *Sebastodes paucispinis* collected 21 May 1964. Azan stain. ED, efferent ductule; SD, sperm duct; STZ, seminiferous tubule zone.

along the posterior third of the testis become filled with sperm to the periphery of the testis, giving the posterior third of each testis a white granular appearance externally (Fig. 5B). The more anterior regions of the testes are dull white to cream colored. With the cessation of spermatogenesis in September and the loss of sperm from mating during later months, the testes shrink. They again become triangular in cross section and are firm and resilient.

Morphology of the Ovaries in *S. paucispinis*

The ovaries in *S. paucispinis* are paired fusiform structures of equal size located in the posterior part of the peritoneal cavity (Fig. 6). Each ovary is an elongate, thin-walled sac filled along most of its length with spongy tissue (stroma and ovigerous tissue), which is attached along a narrow dorsal hilum (Fig. 7). Posteriorly, the paired sacs converge and form a single gonoduct, which lies between the urinary bladder and the intestine and exits through an opening between the urinary pore and the anus (Figs. 2B, 6).

The ovaries are supported along their dorsal surfaces by mesovaria which extend from the ventro-lateral surfaces of the gas bladder. Posterior to the gas bladder, the mesovaria unite with the single median peritoneal fold which supports the urinary bladder and the ovarian duct.

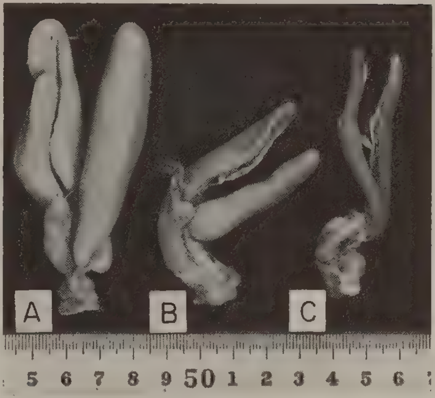

Fig. 5. Urogenital tracts of *Sebastodes paucispinis* males: A. from a 408-mm SL specimen collected 30 August 1963; B. from a 450-mm SL specimen collected 15 December 1963; C. from a 450-mm SL specimen collected 1 March 1964. Note pale enlarged testes of (A) undergoing late spermatogenesis, relative diminution of testes of (B) during mating season, and small dark testes of spent male (C). (Scale in mm.)

The stroma is free from the ovarian wall except for the narrow longitudinal hilum on the dorso-medial surface of the wall. The entire surface of the stroma is characterized by a mosaic of creases which separate easily upon probing and represent the boundaries of transverse lamellae which radiate from the hilum. The structure of these lamellae can be seen in cross sections of the ovaries (Fig. 7). In any such section, several large branches of tissue extend from the hilum. These vascular branches divide into smaller branches which bear the ovigerous tissue.

Arterial System.—The ovaries are supplied by an arterial loop similar to that described for the testes (Fig. 6A). Paired large anterior ovarian arteries extend posteriad from branches of the coeliaco–mesenteric artery. These anterior arteries are supported by anterior extensions of the mesovaria. Upon reaching the ovary each artery penetrates the ovarian wall and courses along the dorso-medial surface of the wall within the longitudinal hilum. This differs from the situation in the males where the spermatic arteries lie dorsal to the testes within the mesorchia. The ovarian arteries give off small lateral branches to the wall and larger ventral branches to the lamellae of the ovary.

The ovaries are supplied posteriorly by the posterior ovarian artery which branches

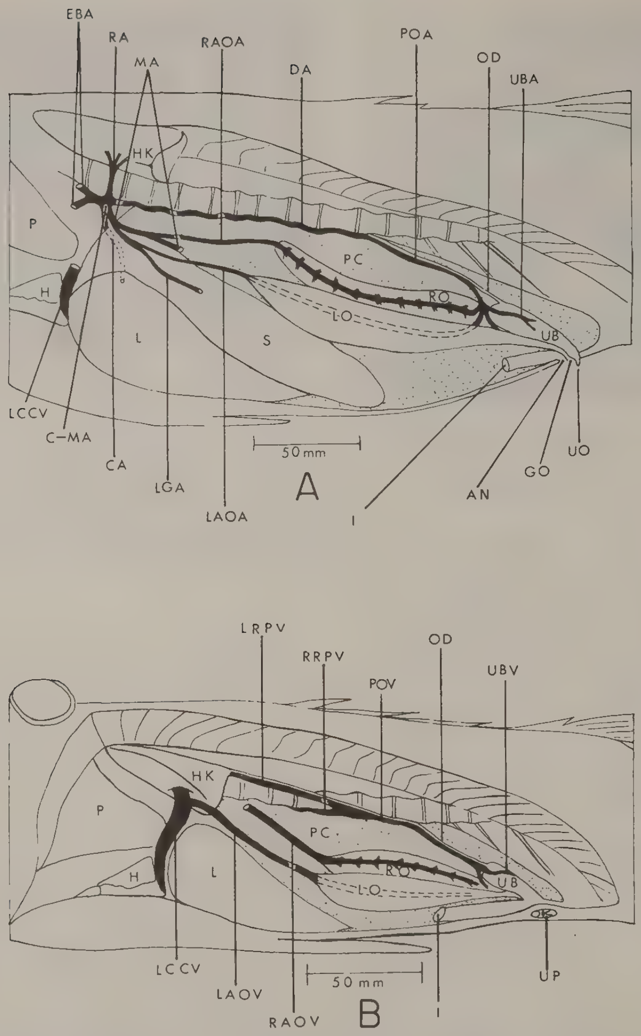
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Fig. 6. Ventrolateral view of female urogenital system of *Sebastodes paucispinis*. A. Arterial system of 558-mm SL specimen collected 6 August 1965. B. Venous system of a 426-mm SL specimen collected 13 July 1965. LAOA, left anterior ovarian artery; LAOV, left anterior ovarian vein; LO, left ovary; POA, posterior ovarian artery; POV, posterior ovarian vein; RAOA, right anterior ovarian artery; RAOV, right anterior ovarian vein; RO, right ovary; RRPV, right renal portal vein. Other labels as in Fig. 1.

ventrally from the dorsal aorta at the 10th or 11th vertebra. At the anterior end of the bladder, the posterior ovarian artery gives off the urinary bladder artery and then turns ventrad to divide immediately into three branches of about equal size. One of these penetrates the wall of each ovary and proceeds anteriad to complete the arterial loop. The third branch proceeds ventroposteriad, dividing into a pair of lateral arteries which supply the paired lateral and single median ovarian ducts.

Thus, as in the males, an arterial loop supplies fresh blood to the ovaries. The anterior ovarian arteries however, are relatively larger than the anterior spermatic arteries.

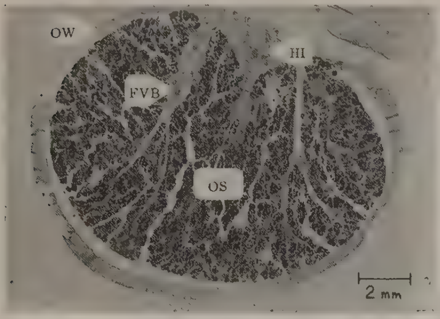

Fig. 7. Cross section of spent ovary of 506-mm SL *Sebastodes paucispinis* collected 1 March 1964. H and E stain. FVB, fibrovascular branch; HI, hilum; OS, ovarian stroma; OW, ovarian wall.

Venous System.—An ovarian vein runs along the dorso-medial surface of each ovary (Fig. 6B). Each vein lies within the hilum of the ovarian wall just beneath the ovarian artery. Small lateral branches are received from the wall of the ovary and larger branches, which drain the stroma, are received ventrally. The anterior ovarian veins depart from the ends of the ovaries and proceed anteriorly with the ovarian arteries. These veins are very large, about equal in size to the paired renal portal veins, contrasting sharply with the small anterior spermatic veins of the males. The anterior ovarian veins separate from the arteries near the transverse septum, penetrate the septum at the ventro-lateral corners of the head kidneys, and enter the medial surfaces of the common cardinal veins just ventral to where they leave the kidneys.

As in the males, a single median vein runs from the anterior end of the urinary bladder and enters the median renal portal vein at about the 10th or 11th vertebra. This vein, however, is very small in females and seems to receive tributaries only from the bladder. No venous branches from the posterior ends of the ovaries could be demonstrated with the latex injections.

Seasonal Changes in the Ovaries of *S. paucispinis*

Changes in Weight.—The ovaries of *S. paucispinis* undergo marked seasonal changes in weight. Monthly changes in the relative weight of the ovaries, expressed as the gonad index, are shown in Fig. 8 for females collected at Newport Beach, California, in 1964. Separate gonad indices were plotted for three categories—spent ovaries, ovaries with maturing ova, and ovaries with developing embryos—since each of these has distinctly separate weight ranges. Ovaries containing ova less than 0.2 mm in diameter were considered as spent and ovaries with ova larger than 0.2 were classed as maturing.

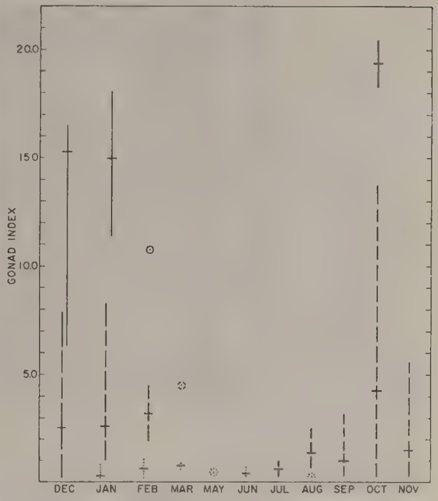

Fig. 8. Gonad indices of *Sebastodes paucispinis* females collected from Newport Beach, California, December 1963–November 1964. Dotted vertical lines indicate ranges of gonad indices for specimens with ova less than 0.2 mm diameter. Dashed lines indicate ranges for specimens with ova undergoing vitellogenesis. Solid lines indicate ranges for specimens containing developing embryos. Horizontal lines represent median gonad index for each month. Single records are circled by the appropriate lines.

During the post-extrusion period, from March to June, gonad indices of females were low. A slightly elevated median gonad index for July was caused by initial vitellogenesis, and gonad indices increased steadily until October when pregnant females appeared in the collections. In November, the collections included only females with maturing ova. Since many of these females had released their first brood, and were maturing a second series of ova, the gonad indices were rather low. Both pregnant females with high gonad indices and spent females with very low gonad indices appeared in January and February.

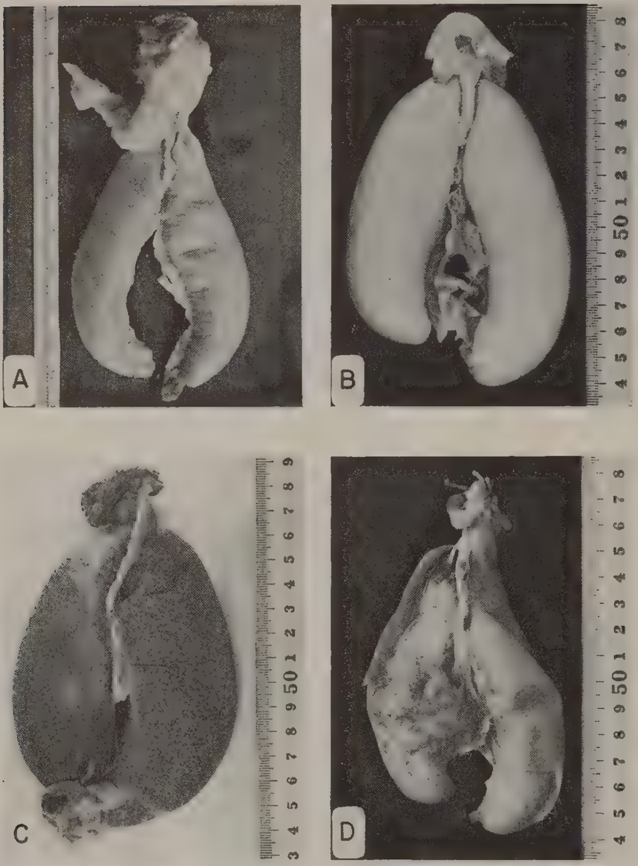

Fig. 9. Urogenital tracts of *Sebastodes paucispinis* females: A. from a 507-mm SL specimen collected 11 July 1964; B. from a 456-mm SL specimen collected 20 November 1964; C. from a 477-mm SL specimen collected 15 January 1964; D. from a 645-mm SL specimen collected 1 March 1964. Note small size, dark color, and thick muscular wall of spent ovaries (A) and relatively large, pale, firm ovaries undergoing vitellogenesis (B). Large gravid ovaries (C) are dark because of melanistic pigment of developing embryos which can be seen through the thin, transparent ovarian wall. Retained larvae lie within ovarian stroma of freshly spawned ovaries (D). (Scale in mm.)

Morphological Changes.—The ovaries are fusiform and have round to elliptical cross sections during the post-extrusion period from March to June (Fig. 9A). The ovarian walls are thick and flaccid. The color of the ovaries during this period ranges from pale pink to dark or grayish red. Retained larvae from the final brood can usually be seen through the ovary wall. They may be alive or in various states of resorption.

Vitellogenesis starts in July and the ovaries begin to enlarge, although they still retain the fusiform shape. The ovarian walls become slightly thinner as the enlarged stroma and ova begin to fill the ovarian cavity. The color of the ovaries during this period ranges from pink to pale yellow. Patches of pale yellow ova contrast with the clear stroma to produce a mottled condition.

Vitellogenesis proceeds throughout August, September, and October and the ovaries become much larger (Fig. 9B). The ovarian wall becomes thin and transparent, revealing the enlarged bright yellow ova beneath. Retained larvae now have been completely resorbed. The ovaries are solid and have a round cross section.

Ovaries with developing embryos first ap-

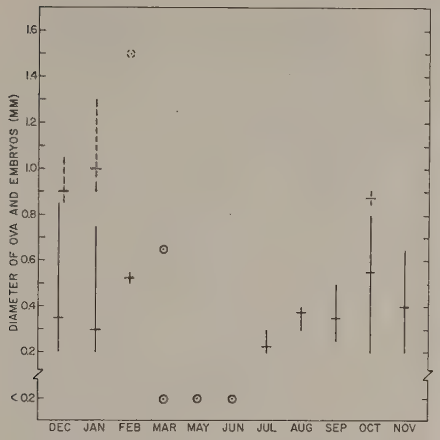

Fig. 10. Diameters of ova (solid verical lines) and embryos (broken vertical lines) of *Sebastodes paucispinis* collected from Newport Beach, California, December 1963–November 1964. Median diameter was determined for several ova or embryos measured from each female. Monthly medians and ranges of these values for all females are represented by horizontal and vertical lines, respectively. Median values for single females are circled.

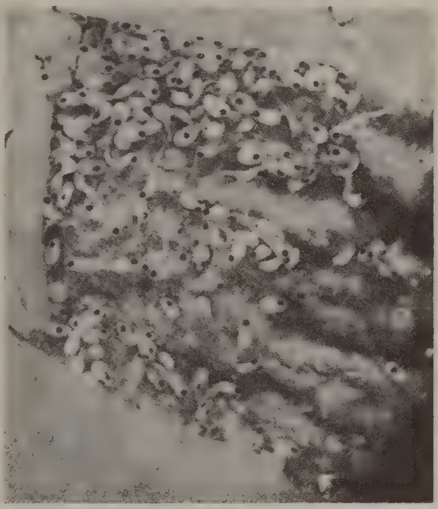

Fig. 11. Ovary of 477-mm SL *Sebastodes paucispinis* collected 15 January 1965. Note brood of advanced embryos and a series of ova undergoing vitellogenesis.

pear in October. These ovaries are translucent yellow, as a result of the clearing of the yolk. Within each pair of ovaries all the embryos of a brood develop at the same rate. As development proceeds, the ovaries continue to enlarge and the translucent yellow, characteristic of early development, becomes paler since yolk is converted into transparent embryonic tissue. When the embryos begin to develop pigmented eyes and body melanophores, the ovaries become a light translucent gray. This gray becomes darker with further embryonic development (Fig. 9C). Ovaries which are ready to release their young are large, black, sac-like structures which distend the peritoneal cavity.

As the embryos develop, the ovaries become more fragile (partially because of the thinning of the ovarian wall), contain much fluid, and are soft. Females with ovaries in this condition may be found from October to March. From November to January, females may be found which have released their first brood of embryos and are maturing a second series of ova. Usually, numerous retained larvae lie in the space between the stroma and the ovarian wall (Fig. 9D). When the second series of ova matures and the retained larvae become resorbed, it is difficult to distinguish such ovaries from those of maturing specimens which have not gestated a brood of embryos.

By March, most of the females have released their second brood. The spent ovaries are grayish red and the size is much reduced. Larvae, and even some large unfertilized ova, retained in these ovaries lie in the space between the stroma and ovarian wall.

Changes in Size of Ova and Embryos.—During the post-extrusion period in 1964 (March to June) the diameters of the unyolked ova were less than 0.2 mm (Fig. 10). Ovum diameter increased with the onset of vitellogenesis in July and continued to increase as vitellogenesis proceeded from July to October. In October the median diameter was 0.55 mm and the range was 0.2–0.8 mm. The values at the lower end of the range represented ova of the second series which were beginning to undergo vitellogenesis.

In 1964, the first pregnant females appeared in October. The median embryo diameter during this month was 0.875 mm, and the range was distinctly higher than that of the ova. Ovum diameter decreased gradually during November, because of an increased percentage of females which had released one brood and were just beginning

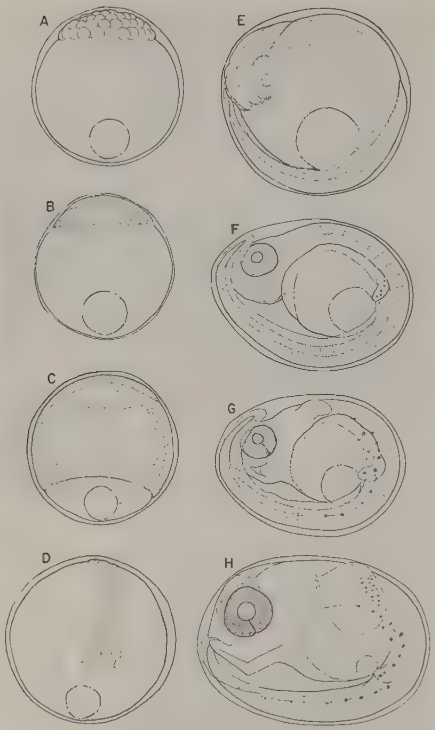

Fig. 12. Intra-ovarian embryos of *Sebastodes paucispinis* taken from different females at various stages of gestation and staged according to Oppenheimer (1937). A. stage 8, 0.94 mm diameter; B. stage 9, 0.90 mm; C. stage 14, 1.0 mm; D. stage 19, 1.0 mm; E. stage 22, 1.0 mm; F. stage 26, 1.6 mm at long axis; G. stage 27, 1.5 mm at long axis; H. stage 32, 2.0 mm at long axis.

to develop a second modal group. The general trends of decreasing ova diameter medians and increasing embryo diameter medians continued into December and January. Greater embryo diameter medians during these months reflected the increased percentage of females with advanced embryos. The ranges of ovum and embryo diameters remained distinct without overlap throughout the months of gestation. The point of separation between the largest ova and the smallest embryos was 0.85 mm.

GONADS OF OTHER SPECIES OF *Sebastodes*

The testes of the 30 species of *Sebastodes* examined were similar to those of *S. paucispinis,* as were the changes in structure, color, and texture which attend the annual gonadal cycle. Each species exhibits its own annual cycle of gonadal activity and undergoes the various maturational stages in a characteristic temporal sequence. Generally, peak spermatogenesis occurs during the summer in those species which, like *S. paucispinis,* gestate and extrude young during fall and winter. Peak spermatogenesis takes place during fall and winter in those species which gestate during spring and summer.

The ovaries of the 30 species were, with one exception, morphologically similar to those of *S. paucispinis*; in *S. diploproa,* one ovary was usually smaller than the other and both were enclosed in the same ovarial sac over most of their length. The changes in ovarian structure and color which accompany the reproductive cycle were basically similar in all species and agree with those described for *S. paucispinis.* Gestation seasons for 9 species of rockfish are shown in Table 1. Some species of rockfish produce more than one brood during a single season. This was first suggested by John S. MacGregor (MS.) who found small numbers of retained larvae within ovaries that also contained maturing ova. In females of some species, I found a brood of advanced embryos or larvae and a series of ova undergoing vitellogenesis; this condition offers direct evidence of multiple brood production (Fig. 11). This direct evidence was found in the following species in addition to *S. paucispinis*: *S. goodei, S. ovalis, S. levis, S. rosaceus, S. constellatus, S. eos,* and *S. chlorostictus.*

DEVELOPMENT OF *S. paucispinis* AND NOTES ON OTHER SPECIES

Intra-ovarian Development.—The youngest brood of embryos was found in a female collected in October 1964 at Newport Beach, California. These embryos correspond to the early high blastula stage of *Fundulus heteroclitus* described by Oppenheimer (1937). The diameters of embryos at this stage are 0.85–1.0 mm. Each has a translucent yolk mass with a single large oil globule ranging from 0.3 to 0.4 mm in diameter. Subsequent developmental stages follow the course described by Oppenheimer; a series of these stages collected from different females is illustrated in Fig. 12.

Melanophores begin to form at a stage corresponding to Oppenheimer's stage 28. First to form is a series of melanophores

TABLE 1. MONTHS OF GESTATION OF VARIOUS SPECIES OF *Sebastodes*. ONLY SPECIES WHICH WERE SAMPLED FREQUENTLY DURING 1963–65 ARE LISTED. Months when pregnant females were captured are indicated by "+" and months when only non-pregnant females were captured are indicated by "—".

Species	Month											
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
S. paucispinis	+	+	+		—	—	—	—	—	+	—	+
S. goodei	+	+	+		—	—	—	—	—	+	+	+
S. levis	+				—		—	—			—	+
S. miniatus	—	—	—		—		—	—			+	—
S. ovalis	+		+		+		—	—			—	—
S. rosaceus	—		+		+		—	—			—	—
S. constellatus	—		+		+			—			—	—
S. chlorostictus	—		—		—		+	—			—	—
S. eos	—	—		+	+	+		—				

along the dorso-lateral surfaces of the gut, followed by a single median series of melanophores along the ventral margin of the tail. These two areas of pigmentation are augmented by additional melanophores as development proceeds. Melanophores develop on the posterior margins of the pectoral fins in the most advanced intra-ovarian embryos (stage 33 or 34 of Oppenheimer).

At parturition, the embryos have functional jaws, eyes, and pectoral fins, and range in length from 4 to 5 mm. Most of the yolk is depleted; what remains is surrounded by the liver. The oil globule persists after the yolk is consumed and is often seen in the youngest larvae collected in plankton samples. In the most advanced broods examined, most of the embryos were hatched or were in the process of hatching, and I believe that this process normally preceeds birth in *S. paucispinis*. Continuous sampling of adult *S. paucispinis* populations suggests that the females gestate the embryos for about one month.

The nutritional and physiological relationships between the pregnant female rockfish and the embryos are of special interest in light of the comparative information available on many other groups of live-bearing teleosts. *Sebastodes* lacks placenta-like connections, in contrast to the situation in many other groups of live-bearing teleosts. After ovulation and fertilization, the developing embryos lie free in the ovarian cavity (Fig. 11), bathed in ovarian fluid. They are, however, surrounded by the empty ovarian follicles whose capillary beds remain intact and functional. Carbon dioxide, oxygen, and nitrogenous wastes must be exchanged between these capillaries and the epithelia of the embryos via the intervening ovarian fluid.

Rates of oxygen consumption determined for embryos of two rockfish species (*S. eos* and *S. rhodochloris*) are shown in Table 2. The Q_{O_2} (µl O_2 consumed/mg dry wt/hr) increases rapidly as yolk is converted to body tissue during development. The Q_{O_2} of

TABLE 2. RATES OF OXYGEN CONSUMPTION OF TWO SPECIES OF ROCKFISH (*Sebastodes*) EMBRYOS AT 11° C.

Species	Developmental Stage (Oppenheimer, 1937)	µl O_2/mg Dry Wt/hr		µl O_2/Embryo/hr	
		Sea Water	50% Sea Water	Sea Water	50% Sea Water
S. rhodochloris	20	0.335	0.364	0.026	0.027
	31–33	1.750	1.474	0.108	0.086
S. eos	31–33	1.056	1.101	0.076	0.072
	34	2.013	—	0.096	—

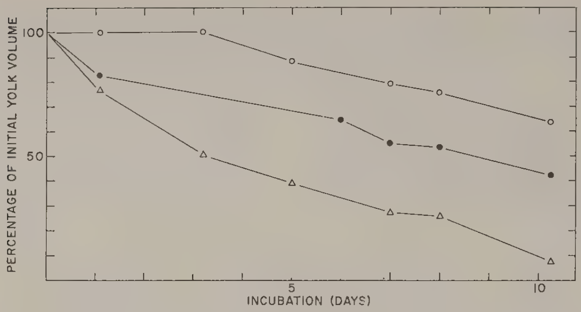

Fig. 13. Effect of temperature on rate of yolk utilization in embryos of *Sebastodes rhodochloris*. Embryos were at Oppenheimer's (1937) stage 20 at beginning of experiment and were incubated in vials of sea water held in a temperature gradient block. Open circle, 8.3° C; solid circle, 13.0° C; open triangle, 18.4° C.

young *S. rhodochloris* embryos (stage 20) is 1/5–1/4 that of the older embryos (stage 31–33). The oxygen consumption of advanced intra-ovarian larvae of *S. eos* with little or no yolk was 0.096 μl/larva/hr.

The effect of temperature on the rate of yolk utilization was determined for embryos of *S. rhodochloris* with the aid of a temperature-gradient block. Individual embryos (stage 20) were placed in test tubes of sea water isotonic to embryonic body fluids and incubated at a series of temperatures ranging from 7.8° to 29.6° C. Change in yolk volume was calculated from daily measurements of the yolk mass after anesthetization of embryos in 0.02% solution of MS-222 (Fig. 13).

Post-natal Development.—Adult *S. paucispinis* were captured during this investigation at a wide range of depths (25–305 m). Since there is no evidence of an upward spawning migration, it is assumed that larvae are born in the normal adult habitat. Ahlstrom (1959) showed that rockfish larvae (*Sebastodes* spp.) inhabit surface waters and have a center of distribution at or above the thermocline. Thus, young extruded from deep-living females must travel a considerable distance upward to reach the larval habitat. Newborn larvae are capable of swimming rapidly with lateral flexion of the tail aided by beating of the pectoral fins. They exhibit positive phototaxis in aquaria and, thus, have a means of orientation. Newborn larvae are buoyant, hence upward migration is aided.

Larvae of *S. paucispinis* collected by CalCOFI during 1953 and 1956 were identified, enumerated, and measured. The stations at which these larvae were collected are shown in Fig. 14. These charts probably define the southern and seaward range of the larvae, but, because of the scanty coverage of stations north of Point Conception, they do not show the northern extent of the distribution. Adults of this species have been taken as far north as Queen Charlotte Sound, British Columbia (Phillips, 1957), and are abundant in northern California waters.

The mean monthly length and abundance of *S. paucispinis* larvae collected at all stations during 1953 and 1956 are listed in Table 3. Larvae first appeared in the plankton in November and December of 1953 and 1956 respectively. Monthly abundance reached a peak during January and February and decreased gradually to June after which no larvae appeared in the plankton tows. Also, the mean length of the larvae increased gradually, reaching a peak in May of both years. The largest larva collected was 24.2 mm SL in 1953 and 29.4 mm SL in 1956. The monthly abundance of planktonic larvae corresponded closely with the seasonal reproductive changes established by examination of adult reproductive tracts during 1963–1965.

The morphological changes in the planktonic larvae of *S. paucispinis* are illustrated in Fig. 15 and morphometric values for a series of *S. paucispinis* larvae are listed in Table 4. The most striking morphological features of *S. paucispinis* larvae are the paired fins. The pectoral fins begin to develop while the embryo is within the ovary and at birth are large and fan-shaped (Fig. 15A). Each fin lengthens rapidly, but the dorsal

TABLE 3. MEAN LENGTHS (MM) OF *Sebastodes paucispinis* LARVAE COLLECTED ON CRUISES OF THE CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS DURING 1953 AND 1956. Numbers of larvae collected each month are listed in parentheses.

	Nov	Dec	Jan	Feb	Mar	Apr	May	June
1953	4.0 (1)	4.5 (22)	5.3 (31)	5.2 (98)	8.2 (25)	10.2 (22)	13.2 (2)	12.2 (3)
1956	—	4.5 (13)	4.9 (43)	5.4 (15)	7.8 (9)	8.4 (6)	15.7 (4)	7.9 (1)

part grows relatively faster than the ventral part, giving the fin an aliform shape. This shape is retained in larvae up to ten mm SL (Fig. 15E), after which the posterior margins again become vertical. The relative length of the fin increases from 10% of the body length at hatching to 40% of the body length in larvae of 13 mm SL, and diminishes to 25% of the body length in the largest larvae. Pectoral rays begin to form in five-mm larvae; the more dorsal rays form first and then progressively the more ventral ones appear. Eight rays are visible in a 5.8-mm larva, 13 in a 7.5-mm larva, and the full complement of 15 rays are developing in a 9.7-mm larva.

The pelvic fins begin to form as small rounded buds in five-mm larvae (Fig. 15B) and, like the pectorals, undergo spectacular development. They lengthen rapidly, and reach a greatest relative length of 40% of the body length in 13-mm SL larvae (Fig. 15G). Like the pectorals, they diminish to about 25% of the body length in the largest larvae. Both soft and spinous pelvic rays begin to form in eight-mm larvae; the full complement of five soft rays and one spinous ray appears in each fin before the larvae are ten mm long.

The caudal fin is the first median fin to develop. It begins as two small ventral thickenings near the tip of the notochord in the smallest planktonic larvae (Fig. 15A). The size of these dense areas increases and they develop into the hypural elements of the fin. Three such elements are forming in a 5.1-mm larva and a total of four hypurals (two superior and two inferior elements) are forming in a 6.6-mm larva. At about seven mm, the tip of the notochord begins to bend dorsad (Fig. 15C). In older larvae, the hypural elements are gradually brought into their final position with their posterior margins perpendicular to the body axis (Fig. 15E).

Caudal fin rays begin to develop in six-mm larvae; the full complement of seven

TABLE 4. MEASUREMENTS OF *Sebastodes paucispinis* LARVAE (MM).

Body Length	Distance snout-anus	Head Length	Snout Length	Length Upper Jaw	Eye Diam	Inter-orbital Distance	Body Depth at Pectoral Fin Base	Pectoral Fin Length	Pectoral Fin Width at Base	Pelvic Fin Length
Before caudal fin formation										
4.6	1.7	1.1	0.3	0.6	0.4	0.4	0.8	0.5	0.4	—
5.1	2.1	1.4	0.4	0.6	0.4	0.6	1.0	0.8	0.5	0.1
5.8	2.5	1.7	0.4	0.4	0.5	0.6	1.2	1.2	0.5	0.2
6.6	2.9	1.9	0.6	0.8	0.7	0.8	1.4	1.4	0.6	0.7
7.5	3.0	2.0	0.6	0.8	0.6	0.9	1.6	1.9	0.7	0.7
8.7	3.6	2.6	0.8	1.0	0.8	1.0	2.0	2.6	0.8	1.5
After caudal fin formation										
9.7	4.9	3.1	1.0	1.5	1.0	1.2	2.6	3.1	0.8	3.1
10.5	5.7	3.9	1.3	1.7	1.2	1.5	3.1	3.6	0.8	3.7
11.5	6.6	4.1	1.3	2.0	1.3	1.6	3.4	4.1	0.9	4.3
13.3	7.2	4.6	1.5	2.4	1.6	1.6	4.1	5.4	0.9	5.0
15.2	9.2	5.4	1.9	2.7	1.8	1.8	4.9	5.0	1.0	5.0
24.2	15.2	8.8	2.9	4.1	2.6	2.4	6.9	8.3	1.3	5.7
29.4	19.0	11.3	2.9	5.1	3.0	2.7	8.1	7.4	1.7	7.3
32.0	19.2	11.7	3.4	4.9	3.0	2.9	8.8	8.3	1.7	7.8

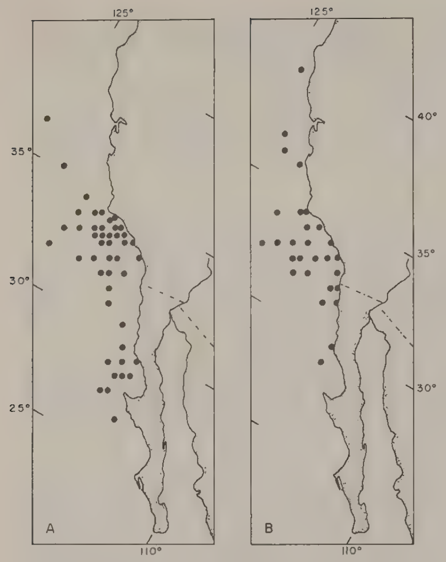

Fig. 14. Stations at which larvae of *Sebastodes paucispinis* were taken during 1953 (A) and 1956 (B) by the California Cooperative Oceanic Fisheries Investigations.

superior and seven inferior principal rays are developing before the larvae reach a length of nine mm. Secondary caudal rays begin to form at nine mm; in the largest larvae, 13 superior and 13 inferior secondary caudal rays are developing (Fig. 15E–H).

The dorsal and anal fins are the last to appear. The radial elements of both begin to develop in eight-mm larvae (Fig. 15D). Soft rays appear in nine-mm larvae and spinous rays can be distinguished in ten-mm larvae (Fig. 15E). Thereafter, development is rapid and the full complement of spinous rays (three in the anal fin; 13 in the dorsal fin) and soft rays (nine in the anal fin; 14 in the dorsal fin) appear in 13-mm larvae (Fig. 15G). The largest larvae have well-developed dorsal and anal fins, similar in proportion to those of juveniles and adults (Fig. 15H).

Another prominent morphological feature of *S. paucispinis* larvae is the development of numerous head spines. The spiny larvae contrast sharply with the juveniles and adults in which nearly all head spines are lacking. The third preopercular spine, which is the first to form, becomes the largest larval head spine. It is first visible in five- to six-mm larvae and elongates rapidly to reach its greatest relative length (35% of the head length) in 10- to 13-mm larvae (Fig. 15B–G). It is serrated during this period. The second and fourth preopercular spines first appear in six-mm larvae. They become prominent and serrated, but do not attain the size of the third spine (Fig. 15C–H). A small spine develops directly anterior to each of these preopercular spines (second, third, and fourth) to form a double row. The small first and fifth preopercular spines do not develop until later in the larval period (Fig. 15G, H). The paired parietal spines develop early in the larval period and attain their greatest size (20% of the head length) in 10- to 13-mm larvae (Fig. 15 E–G). A pair of parietal ridges that run anteriad from the spines begin to form in eight-mm larvae and reach maximum size and serration in concert with the parietal spines. Like the parietal spines, they become greatly reduced during the later larval stages (Fig. 15H). Other spines which develop and regress during the larval period are the tympanics, cleithrals, supracleithrals, nuchals, postoculars, supraoculars, preoculars, suborbitals, and nasals. The only head spines which persist in juveniles and adults are the opercular and preopercular spines.

The melanistic pigment pattern which develops in *S. paucispinis* larvae is a diagnostic character of the species. At birth the larvae have a series of melanophores running from the base of the pectoral fin to the anus along the dorsal margin of the gut on each side of the embryo. This pigment area increases throughout the larval period and later expands to form the peritoneal pigment of juveniles and adults. A single median series of melanistic dashes lies along the ventral margin of the tail. Their number ranges from 6 to 14 (mean of 9 for 20 larvae) and they usually extend from the third or fourth post-anal myomere to the 14th to 17th post-anal myomere. The distance between the melanophores increases posteriorly. These melanophores persist throughout the early larval period but gradually become embedded in the growing hypaxial musculature; they are not visible in larvae longer than ten mm SL. The third and most conspicuous pigment area on newborn larvae is the melanistic margin of the pectoral fin. All of these pigment areas begin to form during intra-ovarian life, as shown in Fig. 12.

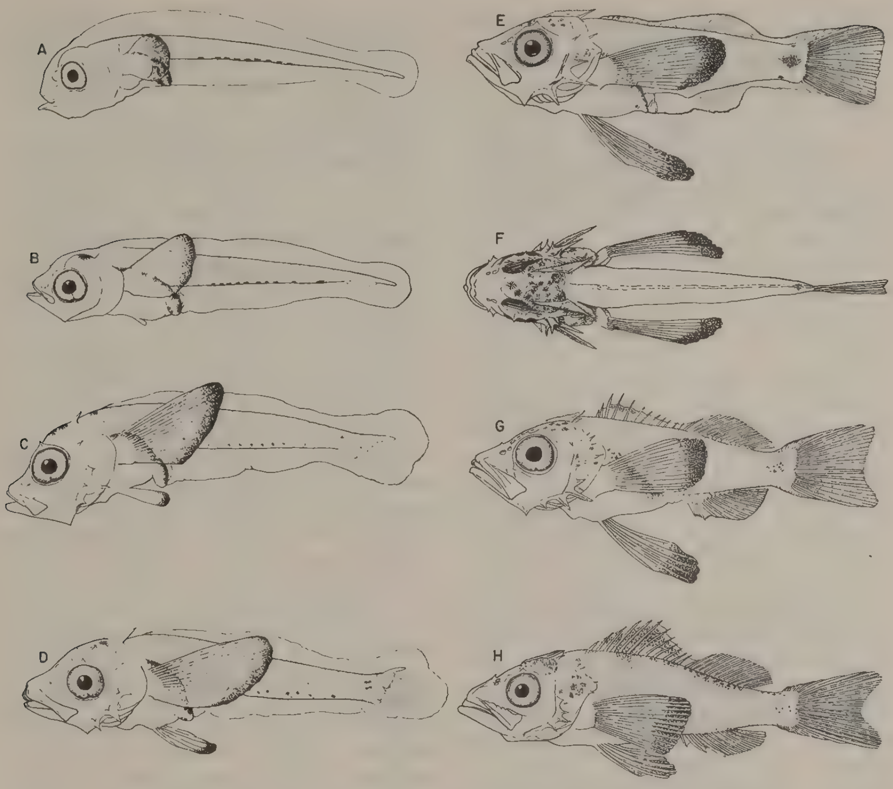

Fig. 15. Planktonic larvae of *Sebastodes paucispinis* mostly from California Cooperative Oceanic Fisheries Investigations plankton samples. A. 4.7 mm; B. 6.1 mm; C. 7.5 mm; D. 8.7 mm; E. 10.5 mm SL; F. dorsal view, 10.5 mm SL; G. 14.0 mm SL; H. 24.2 mm SL.

The pigment patterns of early larval stages of 14 other species of *Sebastodes* are illustrated in Fig. 16. All of these species have a line of melanophores on the ventral midline of the tail and have melanophores on the dorsal surface of the gut. About one-half of the species shown have a line of melanophores on the dorsal as well as the ventral midline of the tail. The number of melanophores in each of these lines is rather constant for each species, and thus affords a useful character for identification (Table 5). Many species have melanophores on the pectoral fins; the pattern of these melanophores and the shape of the fin are helpful in identifying larvae to species. The presence or absence of melanophores on the nape, head, or lower jaw may also serve to identify a species. The melanophore patterns of six species illustrated in Fig. 16J–O are basically similar. Adults of these species also have similar structure and pigment and compose a distinct species complex.

The first additional melanistic pigment to develop in post-natal larvae of *S. paucispinis* is a pair of melanophores above the optic lobes of the brain. These melanophores, and a single median melanophore above the medulla, appear first in five- to six-mm larvae (Fig. 15B). Melanophores are rapidly added in this region and cover all lobes of the brain in ten-mm larvae. The only other major head pigment formed during the larval period is on the posterior part of the operculum. A single opercular melanophore is found in nine-mm larvae, but additional spots are formed rapidly to produce a blotch in older larvae (Fig. 15E–H).

TABLE 5. NUMBER OF MELANOPHORES ON DORSAL AND VENTRAL MIDLINES OF *Sebastodes* LARVAE. Counts were made from 20 individuals of each species.

	Dorsal		Ventral	
Species	$\bar{x}$	Range	$\bar{x}$	Range
S. carnatus	16	11–23	55	49–63
S. chlorostictus			13	11–14
S. constellatus			14	11–17
S. dalli	12	8–17	29	25–34
S. elongatus			17	12–19
S. eos			15	12–18
S. hopkinsi	13	9–18	26	22–31
S. levis			17	13–22
S. macdonaldi			8	6–11
S. ovalis	15	12–18	12	10–15
S. paucispinis			9	6–14
S. rhodochloris			11	8–17
S. rosaceus			12	8–14
S. semicinctus	20	15–23	50	40–63
S. umbrosus			22	17–29

A band of melanophores begins to form at the posterior margins of the pelvic fins in six- to 7-mm larvae (Fig. 15C). This band, along with the corresponding pigment on the pectoral fins, is the most distinctive pigment of *S. paucispinis* larvae. The band widens gradually during the early larval period and rapidly during late larval life. The melanophores cover the posterior third of these fins in the largest larvae (Fig. 16E–H).

Pigment also develops on the caudal fin at an early stage; each side of the developing hypural elements has several melanophores in six- to nine-mm larvae (Fig. 15C, D). In larger larvae the number of these melanophores increases to form a characteristic blotch at the base of the hypurals (Fig. 15E–H).

During the later larval period, after formation of the caudal fin, considerable melanistic pigment appears near and on the dorsal fin. Longitudinal streaks of pigment appear on each side of the fin base in 13- to 15-mm larvae (Fig. 15G, H). One pair of streaks forms at the anterior end of the spinous dorsal and another longer pair of streaks extends posteriad along the bases of the soft rays to the caudal peduncle. Melanistic blotches also develop on the membrane of the spinous dorsal fin. In larger larvae the basal streaks become continuous from the anterior end of the dorsal fin to the caudal peduncle. Saddles of melanistic pigment begin to develop ventrad from these streaks. Three such saddles lie along the spinous part of the dorsal fin and one at the soft-rayed part.

Relatively minor changes of morphology and pigment accompany the transformation of the larva into the juvenile at about 30 mm SL. The cranial spines, which regress during the late larval period, become further reduced, scales appear, and the areas of melanistic pigment present on the older larvae become more extensive. The four dorsal pigment saddles expand ventrad to produce a barred pattern on the trunk above the lateral line. Pigmentation of the pectoral and pelvic fins increases, making the entire distal half of each fin melanistic. A line of melanophores appears along the posterior half of the lateral line. The posterior margins of the hypural elements are delineated by a vertical pigment line. Melanophores appear along the base of the anal fin and on the head, chiefly around the orbit, snout, and symphyseal region of the jaw.

Transforming individuals and juveniles of *S. paucispinis* inhabit shallow coastal waters over rocky bottom in association with algae (*Macrocystis*, *Laminaria*, *Egregia*, and *Eisenia*) or over sand bottom in association with eel grass (*Zostera*), but may also be found in offshore surface waters within floating patches of kelp (*Macrocystis*). Data from collections plotted in Fig. 17 show that juveniles inhabit waters shallower than 20 m during their first year; this has been generally confirmed by direct observations (Limbaugh, 1955; Carlisle, Turner, and Ebert, 1964).

The pigmentation of small inshore juveniles is merely an expansion of the pigment pattern of the larger pelagic larvae. The third and fifth dorsal pigment saddles gradually extend below the lateral line and at about 60 mm SL the juveniles develop a melanistic bar on the distal half of the caudal fin. The resulting barred pattern probably serves as camouflage. These pigment changes are shown in a series of juveniles collected from a drifting mass of kelp (Fig. 18). The barred pattern changes to a punctate pattern in 90 mm SL juveniles; initially the large melanistic spots are distributed all over the trunk and tail of the fish but, as development continues, the spots become restricted to the dorsal region of the body

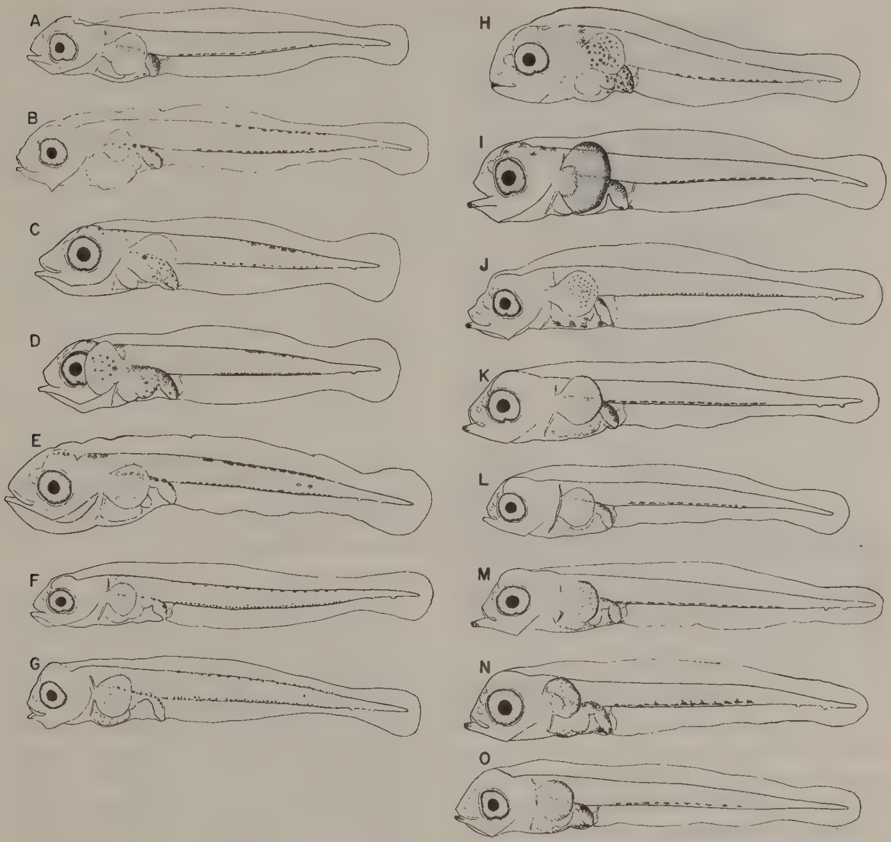

Fig. 16. Early larval stages of various species of *Sebastodes*. A. *S. elongatus*, 4.9 mm; B. *S. hopkinsi*, 4.7 mm; C. *S. ovalis*, 4.7 mm; D. *S. ovalis*, 4.7 mm with pectoral fin reflected to show melanophores at base; E. *S. dalli*, 4.9 mm; F. *S. semicinctus*, 5.5 mm; G. *S. carnatus*, 4.6 mm; H. *S. macdonaldi*, 4.5 mm; I. *S. levis*, 5.0 mm; J. *S. umbrosus*, 4.2 mm; K. *S. rhodochloris*, 4.2 mm; L. *S. rosaceus*, 3.9 mm; M. *S. chlorostictus*, 4.2 mm; N. *S. eos*, 4.0 mm; O. *S. constellatus*, 4.2 mm.

(Fig. 19A). The background pigment of juveniles at this stage is silvery grey. With further growth, they move into deeper waters (Fig. 17) and their pigment changes accordingly. The pigmentation of sub-adults and adults varies greatly with depth, but it is usually solid tan to olive above the lateral line and pink to red below the lateral line. An adult male and female are shown in Fig. 19B and C.

Reproductive Specialization in the Sebastinae

The most remarkable feature of rockfish reproduction, the enormous brood size, is intimately associated with equally remarkable morphological adaptations of the vascular system. The large broods (over two million in the largest females) must place great demands on the maternal arterial system. During vitellogenesis, the ova enlarge from about 0.2 mm to 0.8 mm, largely from the deposition of lipoidal and protein yolk supplied by maternal substrates. Respiratory demands must be high at this time but must be even higher during embryogenesis. The uniformity of size and state of development of the individuals within each brood attest to the precise timing of vitellogenesis, ovulation, fertilization, and development. This

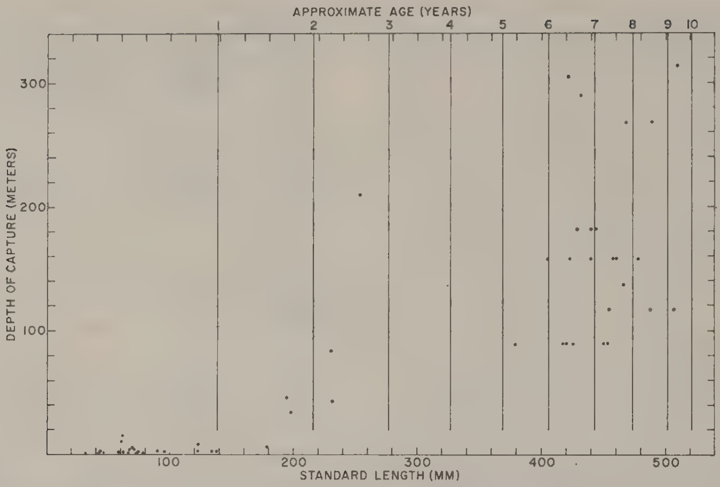

Fig. 17. Depth distribution of *Sebastodes paucispinis* juveniles and adults. Mean standard length of each collection is plotted against depth of capture (mean depth when capture occurred over a bathymetric range). Age groups were computed from data of Phillips (1964).

uniformity requires in turn a large, evenly distributed supply of fresh blood, which is provided by the dual arterial system.

This dual arterial supply to the gonads in *Sebastodes* is a striking departure from the typical situation in teleosts. The large anterior ovarian arteries are the first branches given off by the mesenteric artery upon entering the peritoneal cavity, a fact which emphasizes the importance of their function—to supply fresh blood to the anterior region of each ovary. They are continuous with the posterior ovarian arteries which arise from the dorsal aorta and supply fresh blood to the posterior region of each ovary. Thus fresh blood is distributed evenly along the entire length of each ovary.

Just as oxygen and nutritional demands must be extremely high in maturing and "pregnant" ovaries, rapid production of carbon dioxide and nitrogenous wastes by the large broods must also create a critical situation. The extremely large anterior ovarian veins which provide a direct route through the common cardinal veins to the heart seem to be a remarkable adaptation to this situation. The posterior ovarian vein is very poorly developed so that little or no blood returns to the heart from the ovaries via the renal portal system.

The same advantages imparted by the dual arterial supply to the ovaries are provided by corresponding arteries to the testes, which must be highly active metabolically, especially from June through August during late spermatogenesis. Unlike the situation in the females, where the anterior and posterior ovarian arteries are of equal size, the anterior spermatic arteries are relatively smaller than the posterior spermatic arteries. The relative size of anterior and posterior spermatic veins also contrasts sharply with the condition in females, where most of the blood flows through the anterior ovarian veins. The anterior spermatic veins are very small, whereas the posterior spermatic veins are well developed. The vascular pattern in males may be the more primitive condition and the situation in females may represent further specialization associated with gestation.

To my knowledge the dual arterial gonadal supply of *Sebastodes*, as first described by Allen (1905), is unique among teleosts. There is no report of such a system in other closely related genera of the subfamily Sebastinae (*Sebastes*, *Sebastiscus*), but judging from the general similarity of reproductive processes among these genera, it is reasonable to assume that a similar vascular system exists. Interestingly, a dual venous drainage system was described for *Scorpaenichthys marmoratus*, an oviparous species of the family Cottidae (Allen, 1905). In this species, the posterior spermatic or ovarian veins are the principal routes of blood flowing from the gonads to the heart. Small veins leave the anterior ends of the gonads however, run antero-dorsad in the peritoneal cavity, and enter the posterior cardinal veins. This latter path, although not as direct as in *Sebastodes,* does provide a means of bypassing the portal system of the kidney.

Other structural features of the urogenital system are very similar among the several sebastine genera. Magnússon's (1955) detailed anatomical and histological investigation of the urogenital system of the redfish (*Sebastes marinus*) provides a basis for comparison with *Sebastodes.* I found no fundamental structural differences between the gonads and gonoducts of the two genera.

Recent information concerning the reproductive biology of western Pacific sebastines (*Sebastes, Sebastiscus*) provided by Japanese workers serves as a basis for comparing reproductive processes among the several genera of the Sebastinae. Gonadal cycles in *Sebastes inermis* (Mizue, 1959b, 1964; Mio 1960b), and *Sebastiscus marmoratus* (Mizue, 1957, 1958, 1959a, 1964; Mio, 1960a; Shiokawa, 1962) are essentially similar to those of eastern Pacific sebastines. Ovarian weight increases rapidly in these two species from October to January as a result of vitellogenesis and embryogenesis. Larval extrusion from February to March causes a rapid decline in mean ovarian weight throughout the populations. The male gametogenic cycle for these species slightly anticipates that of the females; the testes attain their greatest size and weight during November, the month of peak spermatogenesis. Thus, as in *Sebastodes,* copulation occurs when the females contain mature or nearly mature ova. A different temporal situation exists in *S. marinus* of the Atlantic where peak spermatogenesis (July and August) precedes the gestation period (March to May) by about six months (Sorokin, 1961). Sorokin proposed that spermatozoa, introduced into the ovaries during August and September, are stored there in a state of physiological rest for four to five months before fertilization and at the proper time are activated by changes in the pH of the ovarian fluid. Although such a temporal sequence was not found in any species of *Sebastodes* reported here, many others remain to be investigated.

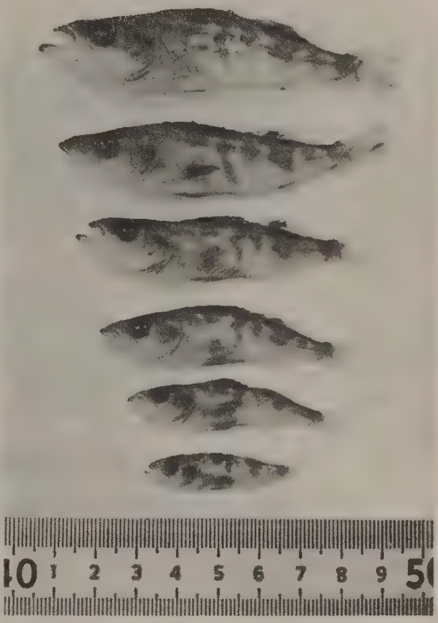

Fig. 18. Juveniles of *Sebastodes paucispinis* collected from drifting mass of kelp 17 June 1964. Specimens range from 35.4 to 74.6 mm SL.

Information is scanty on the gestation time of *Sebastodes.* Eigenmann (1892) estimated a one-month gestation period for *S. rubrivinctus* on the basis of continued examination of gonads from a particular population. No one has followed gestation in any tagged or captive female specimen of *Sebastodes* but several Japanese workers have carried out such observations on closely related genera. Fujita (1958, 1959) found a gestation period of 30 days for *Sebastes oblongus* held at 13.5°–17.5° C and a gestation period of 23 days for *Sebastes pachycephalus nigricans* held at 14.5°–17.0° C. Shiokawa and Tsukahara (1961) observed a gestation period of 20 days in *Sebastes p. pachycephalus* but did not state the temperature of the aquarium water. Tsukahara (1962) found a gestation period of 20–25 days for *Sebastiscus marmoratus* females kept at 15° C. These direct observations agree well with Eigenmann's (1892) estimate of the gestation time for *S. rubrivinctus.* According to my observations *S. paucispinis* has a gestation period of about one month.

Eigenmann (1892) observed that larvae of *S. rubrivinctus* were retained within the

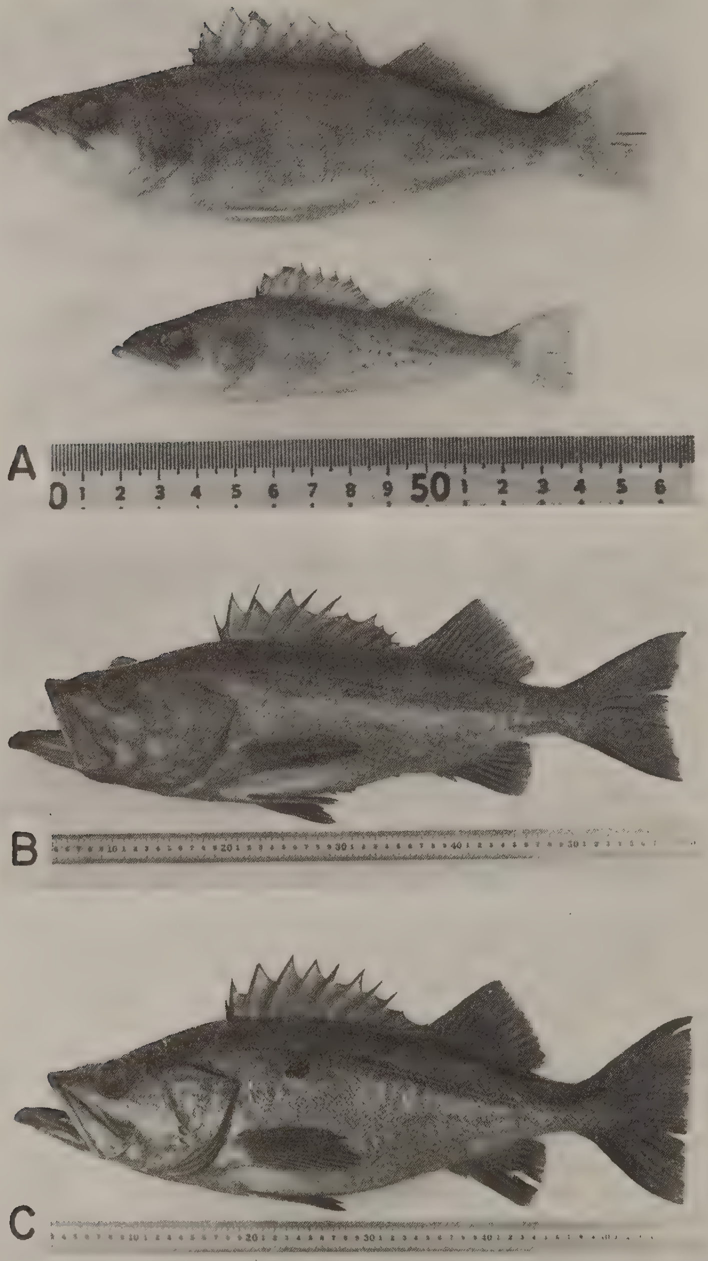
A
0 1 2 3 4 5 6 7 8 9 50 1 2 3 4 5 6
B
C

Fig. 19. A. Juveniles of *Sebastodes paucispinis* (99.1 and 142.5 mm SL) collected 28 November 1964; B. Adult male *S. paucispinis* (472 mm SL) collected 13 July 1965; C. Adult female *S. paucispinis* (478 mm SL) collected 13 July 1965.

ovary some time after hatching. Not all workers have held the same viewpoint regarding the time of hatching. Turner (1942) believed that hatching occurs after birth in *S. caurinus* and Morris (1956) stated that, in *Sebastodes,* embryonic development is completed within the ovary, the unhatched larvae are extruded into the environment, and the exposure to sea water induces hatching.

Some of the controversy surrounding this issue may be caused by the conditions under which the observations have been made. Most rockfish are captured at considerable depth and brought to the surface rapidly. This sudden reduction in hydrostatic pressure permits drastic expansion of the gas bladder, which then exerts considerable mechanical pressure on the viscera, often causing eversion of the stomach. Embryos are often seen flowing from the vents of pregnant females brought onto deck under these conditions. I have observed all stages from newly ovulated ova to hatched larvae flowing from females subjected to these conditions. This extrusion is certainly unnatural and should not be confused with normal birth, which is probably an active process involving contraction of the smooth musculature of the ovarian wall. If prematurely extruded embryos are placed in a vessel of sea water they sink to the bottom. I have observed premature hatching in *Sebastodes* embryos as young as Oppenheimer's stage 20 (optic lobe formation). The osmotic shock of sea water may stimulate hatching, but the increased temperature of the surface water may also be an important factor, since I have induced premature hatching at elevated temperatures in sea water isotonic to the body fluids of the embryos.

The literature contains no report of a captive female *Sebastodes* giving birth although such observations have been made on closely related genera. Fujita (1957, 1958) observed natural birth in captive females of *S. p. nigricans* and *S. oblongus.* The newborn larvae of both species were already hatched, had a small remnant of yolk, and swam freely in the aquarium. Shiokawa and Tsukahara (1961) reported that young of *S. p. pachycephalus* hatch within the ovary 18 days after fertilization and are born about two days later. Tsukahara (1962) stated that young of *S. marmoratus* are born immediately after hatching.

The rate of embryonic development is critically affected by temperature (Fig. 13); thus, the environmental temperature of the brooding female undoubtedly affects the length of the gestation period. Since the known species of *Sebastodes* inhabit a variety of environments from the tide pools to ocean depths greater than 500 m, the separate species are subjected to vastly different temperature regimes. The length of the gestation period, therefore, may vary from species to species and it is probable that deep-living species have longer periods.

Large broods are characteristic of the Sebastinae, but the members of this subfamily differ in the number of broods produced each year. *S. inermis* of Japanese waters produces up to 71,000 young in a single annual brood (Mio, 1960b). The Japanese sebastine, *S. marmoratus* produces several successive broods annually with as many as 20,000 young in each brood (Mio, 1960a). *S. marinus* of the North Atlantic produces a single brood of 40,000–360,000 young annually (Andriyashev, 1954). Although a number of investigators have studied brood size in *Sebastodes* (see Introduction), little attention has been directed to the number of broods produced annually by the various species. My investigations show that some species are multiple spawners and it is likely that other species which were not examined also produce more than one brood annually. Information on this point is essential to meaningful fecundity estimates.

After birth, sebastine larvae occupy surface waters. The end of the larval period must be particularly critical in the life history of the Sebastinae, since the adults are demersal forms that occupy shallow to moderate depths. Transforming individuals fortunate enough to be located in shallow water may safely settle down to their appropriate habitat. Distributional studies reveal, however, that larval sebastines are abundant in oceanic waters hundreds of miles offshore (Ahlstrom, 1961; Henderson, 1961a, b, c). After transformation into the juvenile stage, these individuals are faced with the problem of moving horizontally to shallow areas. The work of Kelly and Barker (1961) suggests that pelagic populations of juvenile *Sebastes marinus* may exist. Similar populations of juvenile *Sebastodes* have not been reported but this lack could reflect inadequate sampling.

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Seasonal Histological Changes in the Gonads of *Sebastodes paucispinis* Ayres, an Ovoviviparous Teleost (Family Scorpaenidae)[1]

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ABSTRACT The elongate paired testes of *Sebastodes paucispinis* consist of tubules which radiate from a single longitudinal sperm duct and terminate blindly at the periphery of the testis. They are lined by an epithelium consisting of columnar cells with distinct elliptical nuclei. During fall and winter, germ cells migrate inward from the fibrous capsule of the testis and become lodged among the tubule-boundary cells of the seminiferous tubules where they mature into primary spermatogonia. Each of these undergoes several mitotic divisions to produce large cysts of secondary spermatogonia. Subsequent spermatogenic divisions within these cysts produce large sperm-filled cysts which rupture, releasing the spermatozoa into the lumina of the seminiferous tubules. Seasonal cycles of cholesterol and carbohydrate production by the tubule-boundary cells suggest that they perform the same functions as the Leydig cells (androgen production) and Sertoli cells (nutrition) of other vertebrates.

The paired fusiform ovaries consist of spongy tissue surrounded by thin-walled muscular ovisacs that converge posteriorly to form a genital duct. The spongy tissue is arranged in transverse lamellae composed of fibrovascular trunks which support epithelial and ovigerous tissue. A series of oocytes (up to 150 μ in diameter) is produced continually from oogonial nests distributed throughout each lamella. Vitellogenesis begins in July and continues throughout the summer. The follicle surrounding the mature oocyte consists of a bilaminar striated vitelline membrane, two epithelial layers (granulosa and theca), and a profuse capillary network.

Spermatozoa appear within the ovaries from October to March. Ovulation probably precedes fertilization since spermatozoa were never found within pre-ovulatory or post-ovulatory follicles. The follicular epithelium regresses after ovulation but the capillary beds remain intact, thus providing a mechanism for fetal-maternal exchange of gases and nitrogenous wastes.

More than 50 species of rockfishes (*Sebastodes* spp.) inhabit the coastal waters of California. For nearly a century, investigators have recognized that all the species in this genus are live-bearers. Information on reproduction of eastern Pacific rockfishes is scanty and their reproductive organs have not been studied histologically (Moser, '67). In contrast, reproduction in certain western Pacific rockfishes has been studied intensively. Mio ('60a,b) described the gross seasonal changes in the gonads of *Sebastes inermis* and *Sebastiscus marmoratus*. Maturational changes in the latter species were also described by Shiokawa ('62). Mizue ('57, '58, '59a,b, '64) has made detailed histological studies of seasonal changes in the gonads of both species. Also, many European workers (Williamson, '11; Lüling, '51; Magnusson, '55; Sorokin, '61) have investigated reproduction in the redfish, *Sebastes marinus*, of the north Atlantic.

This paper describes the general histology of the gonads of *Sebastodes paucispinis* and the seasonal histological changes in the gonads. The production of the annual crops of germ cells in testes and ovaries is described in detail. The gonadal tissue suspected of producing hormones is described and discussed in relation to studies on other teleosts (Hoar, '55; Pickford and Atz, '57; Ball, '60; Dodd, '60). The structural relationship between the maternal and embryonic tissue is defined, allowing certain conclusions on the nature of fetal-maternal exchange.

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[1] A portion of a study submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Department of Biological Sciences, University of Southern California, Los Angeles, California.

MATERIALS AND METHODS

Thirty-six collections of adult *S. paucispinis* were made from December 1963 to January 1965. A total of 209 females and 122 males, 4–10 years old, were collected from Cortes, Tanner, and 43 Fathom Banks off San Diego, California, and from the dory fishery at Newport Beach, California.

Histological preparations were made from the gonads of 107 specimens. All tissues were fixed in 10% formalin, dehydrated in ethanol, embedded in paraffin, and sectioned at 8 μ with a rotary microtome. Sections of all tissues were stained with hematoxylin and eosin, Masson's trichrome stain (Lillie, '40), Heidenhain's Azan stain (Lillie, '54), and with the periodic acid-Schiff (PAS) method (Lillie, '54). Frozen sections of the ovaries and testes of some specimens were stained with Sudan IV and Sudan Black to detect lipids. The Liebermann-Burchardt reaction (Romieu, '27) was used to test for cholesterol in frozen sections of the testes.

General Histology of the testes

The elongate paired testes are located in the posterior region of the peritoneal cavity. A single sperm duct lies along the dorso-medial margin of each testis. These ducts emerge from the posterior ends of the testes and combine to form a median duct which exists through a urogenital papilla.

The general histology of the testes is described from specimens collected between January and May, since spermatogenesis during later months causes marked structural changes. Each testis is enclosed in a squamous mesothelium inside of which is a fibrous tunic. On the dorsal surface of the testis the fibrous layer is thick and encloses the spermatic artery, the spermatic vein, and the sperm duct. Small, longitudinally oriented bundles of smooth muscle fibers are scattered throughout the connective tissue around the sperm duct. The bulk of the testis is composed of tubules radiating from the sperm duct (fig. 1). The tubules which communicate directly with the sperm duct, the "efferent ductules" of Magnusson ('55), branch profusely to form a mass of tubules of slightly smaller diameter, the seminiferous tubules. The seminiferous tubules are oriented at right angles to the long axis of the testis and end blindly at its periphery. A zone of connective tissue, 10–100 μ thick, separates the individual efferent ductules but becomes narrower between the seminiferous tubules and thins to 1 or 2 μ near the periphery of the testis.

The seminiferous tubules are lined with a layer of pale-staining columnar cells, the tubule-boundary cells, which are 10–30 μ high and 7–10 μ wide (fig. 2). The rounded or slightly elliptical nuclei of these cells have a basal position and are 5–8 μ in diameter. They have reticular chromatin and a centrally located nucleolus, 1 μ in diameter. These pale-staining nuclei are easily distinguished from any other nuclei in the testis even when the tubule-boundary cells are distorted during late spermatogenesis. The cells of the efferent ductules are similar to those of the seminiferous tubules. The columnar cells lining the sperm duct are smaller than tubule-boundary cells and have acidophilic cytoplasm and deep-staining nuclei (fig. 3).

The inter-tubular stroma is composed principally of smooth muscle cells, collagen fibers, and blood vessels (fig. 4). The smooth muscle cells form a capsule around each tubule. Collagen fibers are conspicuous chiefly along the bases of the tubule cells but also are found throughout the inter-tubular stroma. Capillaries course throughout the stroma and form a plexus around each tubule.

Seasonal histological changes in the testes

The histological description of the testes given in the previous section did not include the germ cells, which are the dominant element of the testes during certain months. Although some germ cells are present in the testes of *S. paucispinis* at all times of the year, they are most obvious in January near the end of the reproductive season. The tubular structure of the testes is clearly observable at this time, although most tubules contain some sperm produced during the preceding period of spermatogenesis. Scattered germ cells lie in the walls of the seminiferous tubules near the periphery of the testes. The blind ends of the tubules at the periphery of the testes are packed with solid masses of germ cells in various states of transformation into primary spermatogonia (fig. 5). The smallest recognizable germ cells are about 5 μ in diameter. The germ cell at this stage is distinguished by its sharply defined plasma membrane, clear cytoplasm, and deeply stained hemispherical nucleus at the cell margin.

Germ cells appear to migrate centripetally within the inter-tubular stroma, distributing themselves along the seminiferous tubules. Once embedded in the tubule walls, the germ cells begin to enlarge. The clear cytoplasm and sharply defined cell boundaries remain distinct features, but the nuclei become extremely flattened. In germ cells of 10 μ diameter the nuclei appear as crescents at the cell borders. With further cell enlargement the nuclei become more compact, although they remain at the cell margins until the cell diameter reaches 13–15 μ. Nuclei at this latter stage are rounded or of irregular shape with diameters of 5–7 μ.

Further changes in the germ cells chiefly involve the nuclei which enlarge and become reticular. Fully transformed germ cells range from 16–20 μ in diameter and have a pale reticular nucleus which nearly fills the cell. A large 2-μ nucleolus lies in the center of each nucleus. Cells at this stage have been designated previously as resting germ cells, primary germ cells, or primary spermatogonia.

A primary spermatogonium and several earlier germ cell stages are shown in figure 6. Each primary spermatogonium undergoes a series of synchronous mitotic divisions that give rise to at least six generations of secondary spermatogonia. All generations of spermatogonia from a single primary spermatogonium are included in a spherical cyst embedded between the tubule-boundary cells. The progeny of the initial spermatogonial divisions are tinctorially and structurally similar to the primary spermatogonia, although smaller. With successive divisions the nuclei of the spermatogonia become smaller and stain more deeply. Nucleoli cannot be discerned in the nuclei of the later generations, although chromatin strands can be recognized even in the last generation. The diameter of the nucleus of the last generation is about 3.5 μ.

In January although a few small spermatogonial cysts are scattered along the tubule walls, most of the tubules are lined with germ cells in various states of transformation into primary spermatogonia. By March, the walls of the tubules are lined with secondary spermatogonial cysts ranging from 20–50 μ in diameter (fig. 7). Spermatogonial division continues through April and May producing cysts as large as 75 μ in diameter. The tubule lamina begin to close during May as a result of the enlarging cysts, but the tubular structure of the testis remains intact.

In May, cysts of primary spermatocytes begin to appear among the spermatogonial cysts. The marked increase in the size of the nucleus which accompanies the conversion of spermatogonia into primary spermatocytes in other vertebrates generally does not occur in teleost fishes. Primary spermatocytes of *S. paucispinis* (fig. 8) have about the same size as the smallest spermatogonia. Their nuclei are typically 3.5 μ in diameter but may range from 2.5–5 μ. Newly transformed primary spermatocytes can be distinguished by the criterion of Turner ('19) and Hann ('27) who suggested that synezesis (clumping of chromosomes during synapsis) marks the conversion of secondary spermatogonia into primary spermatocytes.

Histological changes are striking in late May and in June. The tubular structure of the testes is less apparent because the bulk of each testis consists of large contiguous cysts, 25–125 μ in diameter, which occlude the lumina of the tubules. The nuclei of the tubule-boundary cells are radically displaced and are usually wedged between the cysts along the basement membranes of the tubules. The cysts are filled with spermatocytes, spermatids, or spermatozoa (fig. 9). Spermatogenesis within each cyst proceeds independently from other cysts. The spherical deeply stained nuclei of secondary spermatocytes range from 2.5–3.5 μ in diameter and have granular chromatin, a feature that distinguishes them from the 2-μ spermatid nuclei which stain solidly with hematoxylin. The transformation of spermatids into spermatozoa follows the course described by Vaupel ('29) for *Lebistes reticulatus*. The spermatozoa have tapered flattened heads 2.5 μ long and 1.5–2 μ at maximal width. An acidophilic mid-piece is followed by a slender tail which is several times as long as the head.

In July and August, the swollen cysts begin to release spermatozoa into the tubule lumina (fig. 10). Filling of the efferent ductules and sperm ducts with sperm indicates a centripetal movement of sperm, presumably as a result of smooth muscle contraction. In the regions of the tubules where cysts have been released into the lumina, the tubule-boundary cells begin to reorganize into a columnar epithelium. The presence of newly encysted germ cells and small cysts of dividing spermatogonia suggests a continuous migration of germ cells into the tubule walls during the summer. Indeed, lens-shaped nests of germ cells are present throughout the summer at the blind ends of the tubules.

Beginning in August, clumps of sperm are found in the single median sperm duct all the way to the tip of the urogenital papilla. Some males in the collections are found in this condition for about six months, but they may not be capable of fertilizing females throughout this entire period since the sperm may be viable for a much shorter time.

Spermatogenesis begins to subside in September and terminates during October. During this period most of the cysts release their spermatozoa into the lumina and consequently the tubule-boundary cells are reorganized as a single columnar epithelium. The connective tissue elements and smooth muscle cells, which were so sparsely distributed between the tubules during late spermatogenesis, now form a dense inter-tubular stroma. The anterior seminiferous tubules gradually become empty as the masses of spermatozoa move posteriorly in the sperm duct. At the posterior ends of the testes the spermatozoa appear to back up into the seminiferous tubules as well as into the efferent ductules since all tubules in this region are completely packed with sperm (fig. 11).

In October, aggregations of germ cells begin to appear in the testicular stroma. These cells will form the basis for spermatogenesis during the following spring and summer. Their nuclei are small, usually elongate, and stain deeply with hematoxylin. The cytoplasm is scanty and hyaline. Germ cells are especially numerous between the blind ends of the tubules, but individual cells are distributed throughout the inter-tubular stroma, apparently in the process of migration inward from the periphery (fig. 12). From October to January these cells appear to migrate centripetally within the inter-tubular stroma. Their encystment and transformation occur serially from the periphery inward. Encysted germ cells are found halfway to the sperm duct in December and January. Most of the sperm have been released by this time and the tubules are reorganized throughout the testes.

The tubule-boundary cells undergo certain histochemical changes which may be related to spermatogenesis. After spermatogenesis has subsided in October, tubule-boundary cells are especially prominent. At this time they are hypertrophied and have relatively clear cytoplasm free of inclusions. From October to March these cells hypertrophy even more and develop numerous basophilic PAS-positive granules and some acidophilic granules (fig. 13). A considerable amount of cytoplasm is sloughed from the tubule-boundary cells into the tubule lumina. From March to May, when the enlarging germ cysts begin to displace the tubule-boundary cells, the large basophilic granules are still present and are especially abundant within the cells of the efferent ductules. At peak spermatogenesis from June to August, when the tubule-boundary cells are confined to the interstices between the swollen cysts, the basophilic granules are rapidly depleted. Periodic acid-Schiff preparations indicate that these granules contain carbohydrate and it is possible that they act as a substrate for the nutrition of gametes.

Small amounts of sudanophilic granules appear in the tubule-boundary cells in October. The abundance of these granules gradually increases as does the affinity for Sudan Black over an 8-month period ending in May. These granules are especially prevalent in the cells of the efferent ductules (fig. 14). During peak spermatogenesis from June to August, sudanophilic granules are absent from the tubule cells.

The sudanophilic granule cycle in the tubule cells is not correlated with the presence of cholesterol in the testes as determined by the Liebermann-Burchardt test. In September and October, cholesterol was detected in the cells of the efferent ductules and in the tubule-boundary cells near the margins of the testes. Amounts of cholesterol decreased during November and December and only traces were evident from January to May. No cholesterol was detected from June to August. The apparent correlation between the maximum production of cholesterol during September and October and the onset of the mating period during these same two months is obvious, cholesterol being a precursor of androgens.

These observations suggest that the tubule-boundary cells of *S. paucispinis* function trophically as well as hormonally and that they may be functionally equivalent to the Leydig cells (andogen-producing cells) and the Sertoli cells (nutritional cells) in other vertebrates.

General histology of the ovaries

The ovaries are paired fusiform structures, each consisting of a mass of spongy stroma and ovigerous tissue enclosed within a thin-walled muscular sac. The stroma is attached dorsally to the ovisac along a narrow longitudinal hilum. The paired ovisacs converge posteriorly to form a single median duct which exits between the anus and the urinary papilla.

The general histology of the ovary is best observed from March to May, since vitellogenesis and subsequent embryo development markedly alter the basic ovarian structure from June through February.

A transverse section of a spent ovary from a female caught in March is shown in figure 15. The outer surface of the ovarian wall is covered by a squamous mesothelium which overlies a fibrous layer 10–50 μ thick. Beneath are an outer circular layer and an inner longitudinal layer of smooth muscle. These two muscle layers form the bulk of the ovarian wall, which is 0.5–1.0 mm thick at this time of year (fig. 16). The two muscle layers are heavily invaded by collagen, and in fact, each muscle cell is enclosed within a fibrous envelope. Lateral branches of the ovarian artery and vein course through these muscle layers. The inner border of the ovarian wall is bounded by a columnar epithelium whose pale basophilic cells are 5–20 μ high.

The ovarian wall is much thicker at the hilum than at other points along its circumference. Here it is composed of large separate longitudinal bundles of smooth muscle cells. The ovarian artery and vein pass through the hilum, sending large branches ventrally into the stroma and smaller lateral branches into the ovarian wall.

The ovarian stroma is arranged as a series of lamellae which are generally perpendicular to the long axis of the ovary. Each lamella is suspended from the hilum by a fibromuscular trunk which contains the major artery and vein serving the lamella. The trunk and its components branch profusely within the lamella to form a dendritic pattern of fibrovascular branches. The surfaces of these branches are covered with oocytes at various stages of maturation, from 5–150 μ in diameter.

Epithelial elements are associated with the branches of the lamellae. The cytoplasm of these cells is inconspicuous, but their nuclei are easily discernible. Two types of nuclei appear in about equal numbers — oval pale-staining nuclei 7–10 μ long and rounded deep-staining nuclei 3–5 μ in diameter. The follicles of the oocytes are formed from these cells; the cells with the smaller nuclei form the granulosa and those with the larger nuclei form the theca.

Oocytes are generated from numerous nests of cells scattered along the branches of the lamellae. These oogonial nests are typically 50 μ in diameter and contain cells at various gametogenic stages (fig. 17). The smallest cells in the nests are oogonia with rounded deep-staining nuclei, 4 μ in diameter, and scanty eosinophilic cytoplasm. As the oogonia develop, the nuclei enlarge and the chromatin becomes reticular.

When oogonial nuclei become 8–10 μ in diameter their individual chromosomes appear and mitotic division begins. The cell diameter at this time is typically 15–20 μ.

Oogonial division occurs throughout the year with no appreciable change in intensity from month to month. Following these divisions the secondary oogonia transform into oocytes. The nuclei enlarge and develop a net-like chromatin reticulum (fig. 18). At synapsis the nuclei are 7 μ in diameter and possess a deeply stained chromatin network which is attached to a large peripheral nucleolus (the "chromatin-nucleolus" of Yamamoto, '56b). The scant cytoplasm of these oocytes is basophilic. Synaptic oocytes in *S. paucispinis* are similar to those found in *Liopsetta* by Yamamoto ('56b) and in *Merluccius* by Hickling ('35).

Further oocyte development involves the enlargement of nucleus and cell diameter, the formation of large peripheral nucleoli, and the development of intensely basophilic cytoplasm. The largest oocytes found within the oogonial nests are about 25 μ in diameter. The nucleus contains one or two large central nucleoli, and several smaller nucleoli are distributed around the periphery.

As the oocytes develop further they move progressively away from the oogonial nests (fig. 19). Small clear vesicles begin to develop in the cytoplasm of 40-μ oocytes. The nuclei at this stage are correspondingly larger (20 μ) and each contains several large nucleoli and many smaller peripheral nucleoli embedded in a pale diaphanous matrix. A continuous series of oocytes from this size to a maximum diameter of 150 μ is present at the margin of the lamellar branches. In each large oocyte clear vesicles are proliferated and become concentrated in a zone surrounding the nucleus.

In 150-μ oocytes the vesicular zone is about 20 μ wide and contains vesicles of varying diameters (fig. 19). The inner vesicles lie along the nuclear membrane. Frozen sections of the ovaries stained with Sudan IV showed these vesicles to be lipoid droplets which dissolved during paraffin preparation. The nuclei of these larger oocytes are about 100 μ in diameter and contain small peripheral nucleoli with a maximum diameter of 5 μ. The eosinophilic nucleoplasm contains "lampbrush chromosomes" centrally.

The follicle of the oocyte begins to develop while the oocyte is still in the oogonial nest. The initial follicular cells, recruited from the epithelial cell complement with small deep-staining nuclei, become appressed to the plasma membranes of 40-μ oocytes. As the oocyte enlarges and moves away from the oogonial nest, additional cells are added to the developing granulosa. Also, the epithelial cells of the stroma which are characterized by their large pale-staining nuclei move to the surface of the enlarging oocytes and begin to form a thecal layer immediately outside the granulosa. The first evidence of a follicular vascular network appears in 100-μ oocytes where capillaries begin to penetrate the space between the two follicular epithelial layers. A well-formed capillary plexus is present in 150-μ oocytes.

All of the developmental stages described were found in ovaries examined during all months of the year. The continuous series of oocytes up to a diameter of 150 μ, found even in gravid ovaries, serves as a reservoir for successive modes of maturing oocytes.

Seasonal histological changes in the ovaries

Secondary yolk formation (vitellogenesis) begins in July when the 150-μ oocytes enlarge synchronously to form a discrete mode. A female captured during July, 1964 had a mode of oocytes at about 200 μ in diameter with nuclei 75–100 μ in diameter (fig. 20). In these oocytes the nuclear membrane is distinct and intact. Nucleoli, 3–7 μ in diameter, are distributed around the inner margin of the nuclear membrane. The granular nucleoplasm is eosinophilic and contains lampbrush chromosomes. The cytoplasm remains basophilic but is paler and more vesicular than previously. Yolk-globule formation is initiated in oocytes of this size in a cortical zone of the cytoplasm. Yolk globules have diameters from 1–5 μ and stain either red or blue with Masson's trichrome stain. These globules give fresh oocytes a yellow color.

A narrow zone of cytoplasm separates the yolk-globule zone from the plasma membrane in 200-μ oocytes. Outside the plasma membrane lies the developing vitelline membrane which stains bright blue with Masson's trichrome stain. The vitelline membrane is surrounded by the follicle which has now become structurally more complex. The cells of the innermost epithelial layer, the granulosa, have a deep-staining reticular nucleus surrounded by a stellate cytoplasmic mass. Cytoplasmic extensions appear to connect neighboring cells. A well-defined basement membrane adjoins the outer border of the granulosa. A capillary plexus interposed between the granulosa and the outer follicular layer (theca) has undergone considerable proliferation. The theca is composed of a single layer of squamous cells with large flattened pale-staining nuclei 7–12 μ long. The cell boundaries are best observed in tangential sections, where they appear as contiguous hexagons each about 15 μ in diameter. A basement membrane lies along the outer border of the thecal layer.

Further maturational changes were evident in the 300- to 400-μ oocytes of a female collected in August 1964. The nuclei of these oocytes are larger but remain structurally similar to those of 200-μ oocytes. The cytoplasm continues to change during this period. Yolk vesicles and globules occupy most of the cytoplasm except for a narrow pale basophilic zone around the nucleus. A zone of lipoidal yolk vesicles extends from the border of this peri-nuclear zone to the periphery of the cytoplasm, where it intermingles with the yolk-globule zone. The yolk globules are spherical, range up to 10 μ in diameter, and stain a brilliant red with eosin and with Masson and Azan techniques.

Vitellogenesis had proceeded further in some females collected in September, 1964. In one female with an advanced mode at diameters of 400–500 μ the centrally located nuclei are as large as 150 μ in diameter (fig. 21). The large peripheral chromatin-nucleoli contain pale-staining vacuoles. The bulk of the cytoplasm is occupied by a mass of lipoidal vesicles interspersed with large yolk globules that extends from the nucleus to the plasma membrane. The yolk globules are slightly larger than in 300- to 400-μ oocytes and range up to 15 μ in diameter. The thickened vitelline membrane is now acidophilic and is developing radial striations.

Oocytes were nearing maturity in some females collected during October 1964. A series ranging from 550–700 μ was found in one female (fig. 22). Although the nuclei remain centrally located, several changes are evident. The large chromatin-nucleoli begin to migrate away from the nuclear membrane towards the center of the nucleus, and the pale vacuoles within these nucleoli enlarge. The nuclear membrane starts to break down. The lipoid vesicles begin to coalesce to form vesicles as large as 100 μ in diameter. The yolk globules start to break down into an amorphous substance which stains deep blue with Masson's technique and bright blue in Azan preparations. Disintegration of the yolk globules, which begins at the periphery of the oocyte and proceeds centrally, is coincident with the change from opaque to translucent yellow in fresh oocytes.

The follicles of the mature oocytes shown in figures 23 and 24 consist of the following concentric structures: (1) a bilaminar striated vitelline membrane 2 μ in thickness lying next to the plasma membrane of the oocyte; (2) a single inner epithelial layer, the granulosa; (3) a basement membrane associated with the granulosa; (4) a profuse capillary network filled with erythrocytes; (5) a single outer epithelial layer, the theca, consisting of squamous cells with nuclei larger and paler than the granulosa nuclei; (6) a basement membrane associated with the theca.

All previous microscopical studies of teleost ovaries have revealed the thick striated vitelline membrane surrounding the mature oocyte. This membrane has been designated variously as the zona radiata, corona radiata, zona pellucida, oolemma, or chorion. Jollie and Jollie ('64) described the fine structure of this membrane in *Lebistes reticulatus* from electron micrographs. The vitelline membrane in *Lebistes* consists of an inner layer of amorphous material perforated by pore canals. Microvilli project from the surface of the oocyte, penetrate through each of these pore canals, and develop an intimate association with the inner epithelial layer of the follicle. The massed endings of these microprojections which pass through the pore canals impart a bilaminar appearance to the vitelline membrane. The microvilli greatly increase the surface area of the oocyte and must enhance the exchange of materials between follicle and oocyte. Although my observations were limited to light microscopy, the vitelline membrane in *Sebastodes* is structurally similar to that of *Lebistes* in a gross sense and therefore probably has a similar microstructure.

The stroma surrounding the mature oocytes is sparse. The oogonial nests are scattered among the large oocytes within the lamellae and are still actively produring oogonia by mitotic divisions. Transformation of oogonia into primary oocytes continues within the oogonial nests, and a series of primary oocytes ranging up to 150 μ in diameter remains within the stroma.

The collections contained no examples of the more advanced stages of oocyte maturation, including the migration of the nuclear material to the periphery and the meiotic divisions. Since follicles of the most advanced oocytes found during October were undergoing structural disintegration, it is likely that ovulation precedes these final maturational processes.

Spermatozoa appeared in the histological sections of the ovaries of more than half of the females collected during October 1964. They were found singly or in clumps embedded among the epithelial cells between the maturing oocytes or on the outer surfaces of the follicles (fig. 23). Sperm were never found within the follicles of oocytes or within follicles vacated after ovulation. Thus, oocytes are probably fertilized soon after ovulation by spermatozoa which are distributed throughout the surrounding stroma.

In some of the females collected during October 1964, fertilization had taken place and a brood of embryos (blastula stage) was present. The embryos lie in the ovarian cavity free from the empty follicles (fig. 25). The blastodiscs of the embryos consist of rounded basophilic cells. The bulk of the embryo is a continuous fluid yolk mass which stains purple with eosin-haematoxylin and with PAS but capriciously red or blue in trichrome preparations (Azan and Masson techniques). A single large oil vesicle, produced by the coalescence of the many small lipoid vesicles, lies near the periphery of the yolk. A peri-vitelline space separates the embryo from the vitelline membrane or chorion. The chorion is only 1 μ thick following fertilization and does not appear radially striated, although tangential sections reveal its porous nature.

The stroma surrounding the embryos is composed chiefly of empty follicles. Although the epithelial layers of the empty follicles retain their structural integrity, certain cytological changes occur in these layers following ovulation (fig. 26). The deep-staining granulosa nuclei contract into spheres 3–4 μ in diameter. The pale thecal nuclei which were flat in the mature oocytes are now elliptical and range in length from 5–7 μ. The capillary network between the theca and granulosa remains intact and filled with erythrocytes. The absence of extra-vascular erythrocytes in the ovary indicates that ovulation does not rupture the capillaries, which at this stage are well dispersed among the embryos and constitute an excellent mechanism for gas and waste exchange. As the brood of embryos develops, the epithelial layers collapse and the follicular lumen is obscured, but the capillary plexus appears to remain functional. A second group of oocytes begins vitellogenesis when the embryos of the first brood reach the stage of eye-lens formation (fig. 27). This new group is recruited from the 150-μ oocytes of the residual supply always present in the ovary.

Extrusion of the initial brood begins in November. Some females collected at Newport Beach late in November 1964 already had a well-developed second mode of oocytes (400–500 μ). Extrusion of the second brood is completed by January or February. Following the extrusion of the second brood, the ovaries undergo considerable histological change. The empty follicles of the second brood, like those of the first, collapse and lose their structural integrity. The capillary beds of these follicles are still intact and filled with erythrocytes, giving fresh ovaries of this stage a deep red color. In time, these capillary beds are resorbed. The series of residual oocytes (ranging up to 150 μ) is still present but depauperate, as a result of the recruitment for two broods of young. Mitotic division of oogonia and primary oocyte formation continue within the oogonial nests throughout the post-extrusion period, thereby replenishing the series of residual oocytes.

Degenerating oocytes which have failed to reach maturity are prominent in the ovaries of all spent females. In some females an entire series, perhaps the third one, is atretic (fig. 28). This atresia, however, is not restricted to spent ovaries. During the maturation period some oocytes of each mode undergo oolysis and degenerate in a regular fashion. Oocytes are much advanced (usually larger than 400 μ) before this breakdown occurs. The first stages of oolysis involve degeneration of the nucleus and vitelline membrane and the liquefaction of the yolk globules that form the bulk of the cytoplasm. The granulosa remains as a single epithelial layer but the cells become greatly hypertrophied. Their cytoplasm is filled with droplets of various sizes up to 15 μ, which stain either red or blue with Masson's technique. The degenerating cytoplasm of the oocyte may also contain some red- and blue-staining yolk droplets but consists chiefly of a dark purple liquefied yolk mass (fig. 29). Small lipoid vesicles lie in irregular clumps throughout the yolk. Apparently the granulosa cells are athrocytic since the yolk is depleted, whereas the granulosa cells are filled with yolk-like droplets. During this process the walls of the follicles collapse, but the granulosa retains its structural integrity. Melanistic granules often develop throughout the degenerating yolk mass, particularly in association with the lipoid vesicles.

Most of the yolk is resorbed in the atretic follicles by the time the other oocytes of the same mode have matured and have been ovulated. After the depletion of most of the yolk, the cells of the granulosa separate and invade the remaining cytoplasm of the oocyte, now chiefly a mass of lipoid droplets and fine granular yolk. Typically, remnants of the vitelline membrane are also present. Occasional capillaries from the original follicular plexus penetrate the degenerating yolk. The resultant mass of tissue consists of numerous granulosa cells filled with pale-staining granules and occasional yellow or orange vesicles (fig. 30). The cytoplasmic granules of the cells stain pale green, blue, or red with trichrome preparations and are strongly PAS-positive. The nuclei of these cells are small (3–5 μ) and closely resemble the granulosa nuclei of the surrounding stroma. Melanistic granules are often very numerous within the atretic bodies (fig. 30).

Atretic follicles are formed from the second mode of oocytes in the same way as from the first mode. The characteristic masses of tissue which result from this atresia remain in the ovaries throughout the post-extrusion period, and some are present in the developing ovaries during the following reproductive season.

DISCUSSION

Certain aspects of teleost spermatogenesis differ strikingly from the pattern typical of other vertebrates. The literature shows little agreement regarding the annual origin of male germ cells. Turner ('19) described the migration of germ cells into the lobules of the testes from certain extra-testicular cell cords in the yellow perch, *Perca flavescens*. Subsequent investigators failed to find extra-testicular cords of germ cells in other species although some have described migration of germ cells within testes (Foley, '26, in *Umbra limi;* Jones, '40, in *Salmo salar;* Gokhale, '57, in *Gadus merlangus* and *G. esmarkii*).

Other workers have reported that the annual crop of germ cells originates from residual cells which do not undergo spermatogenesis during the preceding spawning season. A number of teleosts are included in this group: *Gambusia affinis* (Geiser, '22); *Gasterosteus pungitius* (van Oordt, '24a); *Cottus bairdi* (Hann, '27); *Gasterosteus aculeatus* (Craig-Bennett, '31); *Betta splendens* (Bennington, '36); *Fundulus heteroclitus* (Matthews, '38); *Phoxinus laevis* (Bullough, '39); *Salmo gairdneri* (Weisel, '43); *Clupea harengus* (Bowers and Holliday, '61).

Extra-testicular cords of germ cells were not found in *Sebastodes paucispinis*, but the annual migration of germ cells inward from the fibrous envelope of the testis is described in this paper. The question of how these germ cells are proliferated remains unanswered. Although mitotic division of the germ cells in the fibrous capsule was never observed, the cells might be continually replenished by amitotic division.

It has long been established that the testes of teleosts produce androgens (Pickford and Atz, '57), but the site of androgen production within the testis has been a matter of much controversy (Courrier, '21, '22, '25; Champy, 23a, b; van Oordt, '24b, c; Craig-Bennett, '31). Perhaps the most important contributions to the controversy regarding the interstitial tissue of teleosts are the histological and histochemical studies of Marshall and Lofts ('56) and Lofts and Marshall ('57). They proposed that the testes of teleosts can be differentiated into two basic structural types. In the first category (*Gasterosteus, Tilapia, Clupea*) the tubules or lobules are formed by fibrous connective tissue and the interstitial cells are located between the tubules. In the second type (*Esox, Labeo*) the lobules or tubules are bounded by cells, the lobule- or tubule-boundary cells, and no interstitial cells are present. They hypothesized that both the interstitial cells and lobule-boundary cells perform the function of the Leydig cells of other vertebrates. This conclusion was based on their discovery that the lobule-boundary cells of *Esox* undergo a seasonal production of cholesterol-positive lipids in a pattern similar to that of avian Leydig cells. They found a steady accumulation of lipid inclusions within the lobule-boundary cells during the three months preceding spawning and during the 3-month spawning run. At the end of spawning, the inclusions were gradually discharged into the lumina of the lobules, leaving the cells free of lipids for several months.

Although the seasonal production of sudanophilic material in the tubule-boundary cells of *Sebastodes paucispinis* does not correspond to that described for *Esox* by Lofts and Marshall ('57), the appearance of cholesterol in the tubule cells at the beginning of the mating period suggests that these cells are involved in androgen production. The fact that these cells also produce PAS-positive granules in a cycle seemingly related to spermatogenesis suggests that they perform a nutritive function as well as a hormonal one.

Several viewpoints exist regarding the annual source of gametes in female teleosts. Brock ('78), who examined a large number of teleosts, believed oocytes originated from single epithelial cells in the ovarian stroma. Calderwood ('92) described ovarian cycles in several teleosts and suggested that oocytes originated from the coalescence of 10 to 12 epithelial cells. Wheeler ('24), on the other hand, found the source of oocytes in *Pleuronectes limanda* to be certain follicle cells which undergo transformation. Yamamoto ('56a) observed a similar situation in another flatfish, *Liopsetta obscura*. No such transformation of epithelial or follicle cells was observed in *Sebastodes*. All maturing oocytes originate from the oogonial nests and are produced by continuous oogonial mitotic divisions.

Hann ('27) stated that oogonia in *Cottus bairdii* became lodged in cell nests early in the period of sexual differentiation and produced the annual crop of oocytes through subsequent mitotic divisions. Only a portion of the secondary oogonia developed into oocytes each year and a reserve supply of oogonia was always present. A similar situation prevails in *Sebastodes paucispinis*. Although oogonial division is continuous throughout the year, some of the daughter oogonia fail to mature into primary oocytes and thus remain in the cell nests as progenitors of more oogonia.

The formation of "pre-ovulatory corpora lutea" from degenerating oocytes has been observed in the ovaries of all teleosts that have been carefully examined histologically (see reviews by Hoar, '55; Pickford and Atz, '57; Ball, '60; Dodd, '60). Since the production of progesterone by the mammalian corpus luteum is essential for the initiation and maintenance of pregnancy it is particularly tempting to imagine an analogous function for the pre-ovulatory corpora lutea of viviparous teleost fishes. Wallace ('03) noted the hypertrophy of granulosa cells in degenerating follicles of *Zoarces viviparous* but emphasized their lack of resemblance to the corpora lutea of mammals. Also, after the ovulation of the normal oocytes in *Zoarces*, the granulosa becomes hypertrophied (Stuhlman, 1887; Bretschneider and Duyvené de Wit, '47) and, although these follicles may be a source of progestational hormone, they appear to function chiefly in the production of nutritive fluid. Stolk ('51, '57) described the histogenesis of pre-ovulatory corpora lutea in *Lebistes reticulatus* and *Dermogenys pusillus*, two species which have repetitive month-long gestational cycles. During the gestation of one brood in these species, the oocytes of the next brood are maturing. Pre-ovulatory corpora lutea are produced in well-defined cycles during each gestation. In *Sebastodes*, oolysis takes place during vitellogenesis in all females and, as in other viviparous teleosts, the resultant pre-ovulatory corpora lutea may be a source of progestational hormones.

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PLATES

Abbreviations

AO, atretic oocyte
BD, blastodisc
C, capillary
CSM, circular smooth muscle
ED, efferent ductule
EF, empty follicle
FVB, fibrovascular branch
GC, germ cell
GN, granlosa cell nucleus
HG, hypertrophied granulosa
HI, hilum
LCH, lampbrush chromosome
LG, lipoid granule
LSM, longitudinal smooth muscle
LU, lumen
LV, lipoid vesicle
MO, maturing oocyte
MP, melanistic pigment
NL, nucleolus
OCC oocyte cytoplasm
OCN, oocyte nucleus
OGN, oogonial nucleus
ON, oogonial nest
OS, ovarian stroma
OW, ovarian wall
PG, PAS-positive granule
PSC, primary spermatocyte cyst
PSG, primary spermatogonium
RBC, erythrocyte
RO, residual oocyte
SA, spermatic artery
SD, sperm duct
SDE, sperm duct epithelium
SGC, secondary spermatogonial cyst
SMN, smooth muscle cell nucleus
SN, synaptic nucleus
SSC, secondary spermatocyte cyst
ST, seminiferous tubule
STC, spermatid cyst
SV, spermatic vein
SZ, spermatozoa
SZC, spermatozoa cyst
TBC, tubule-boundary cell
TCN, tubule-boundary cell nucleus
TN, theca cell nucleus
VM, vitelline membrane
YG, yolk globule

PLATE 1

EXPLANATION OF FIGURES

1 Cross-section of testis of 410-mm *Sebastodes paucispinis* collected May 21, 1964. Azan stain. 10.8 ×.

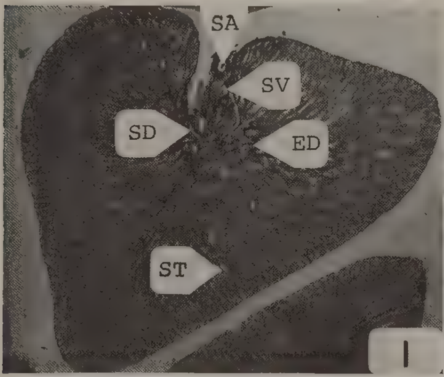
2 Cross-section of seminiferous tubule of 410-mm *S. paucispinis* collected March 1, 1964, showing tubule-boundary cells with their distinct nuclei. Masson's trichrome stain. 500 ×.

3 Cross-section of sperm duct of same specimen shown in figure 2. Masson's trichrome stain. 500 ×.

4 Inter-tubular connective tissue of same specimen shown in figure 2. Masson's trichrome stain. 1250 ×.

5 Cross-section at periphery of testis of 343-mm *S. paucispinis* collected January 4, 1964, showing nests of germ cells at blind ends of tubules and other maturing germ cells embedded along tubules. Masson's trichrome stain. 125 ×.

6 Longitudinal section of seminiferous tubule of 445-mm *S. paucispinis* collected January 15, 1965, showing mature germ cell (primary spermatogonium) embedded in tubule epithelium. Masson's trichrome stain. 500 ×.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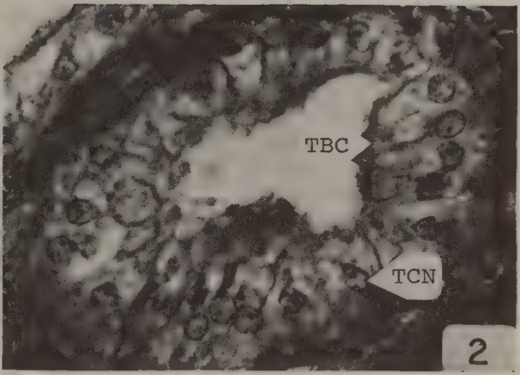
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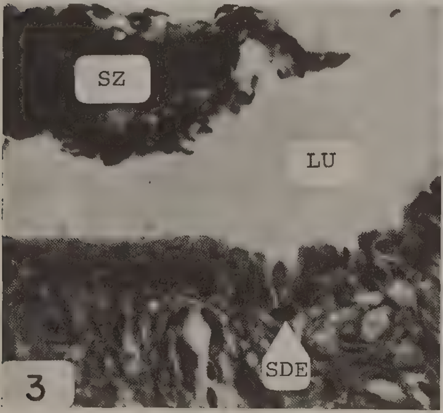
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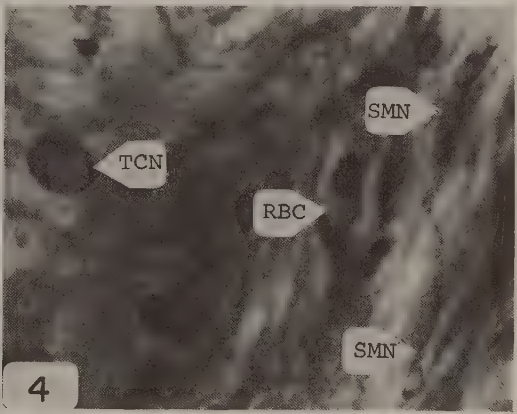
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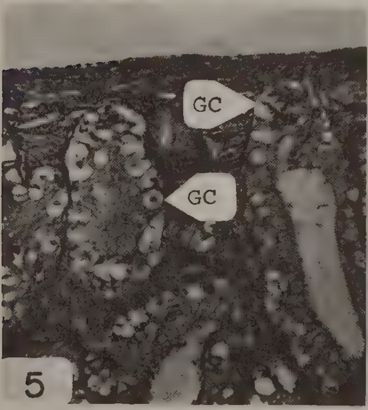
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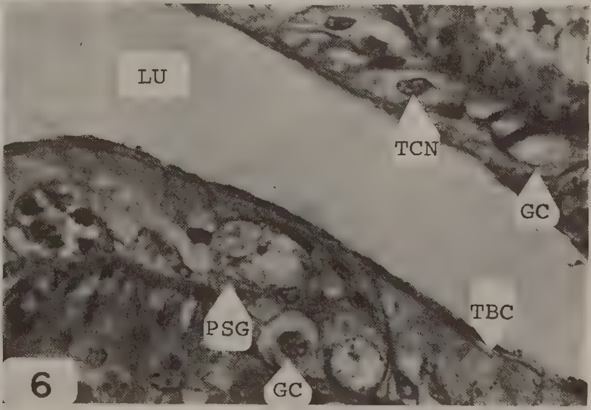
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PLATE 2

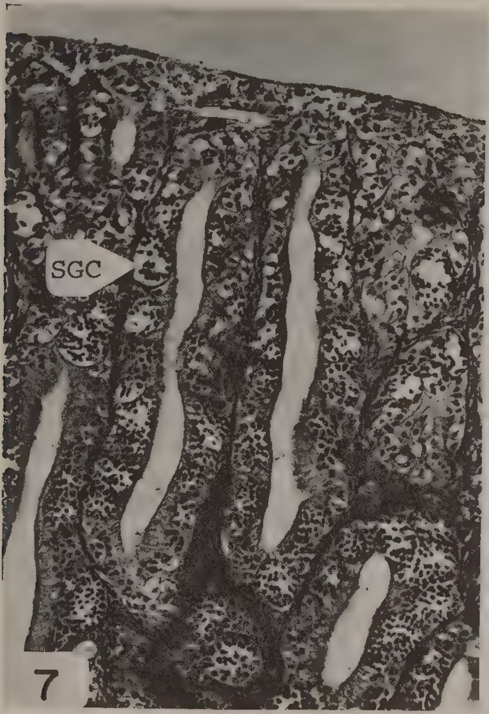
EXPLANATION OF FIGURES

7 Cross-section near periphery of testis of 450-mm *S. paucispinis* collected March 21, 1964, showing cysts of secondary spermatogonia embedded in tubule walls. Masson's trichrome stain. 125 ×.

8 Section of seminiferouus tubule of 432-mm *S. paucispinis* collected June 20, 1964, showing various stages of spermatogenesis in contiguous cysts. Masson's trichrome stain. 500 ×.

9 Longitudinal section of seminiferous tubules of 432-mm *S. paucispinis* collected June 6, 1964. Each cyst contains gametes at same maturational stage. Most tubule lumina are closed by swollen cysts. Masson's trichrome stain. 125 ×.

10 Rupture of cysts containing spermatozoa in testis of 467-mm *S. paucispinis* collected August 22, 1964. Masson's trichrome stain. 125 ×.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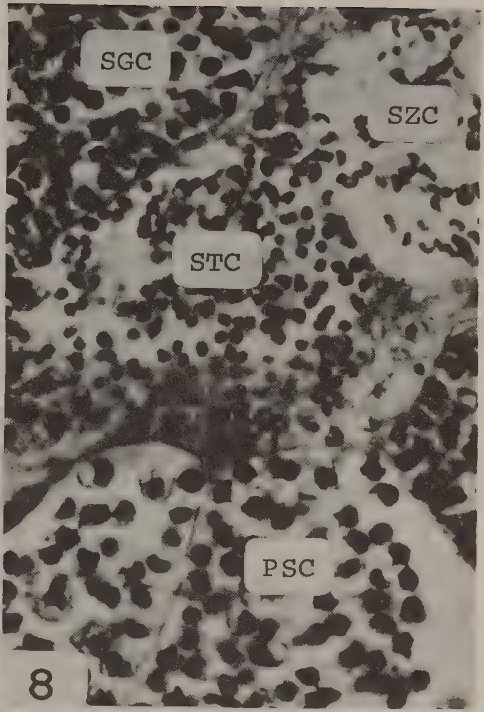
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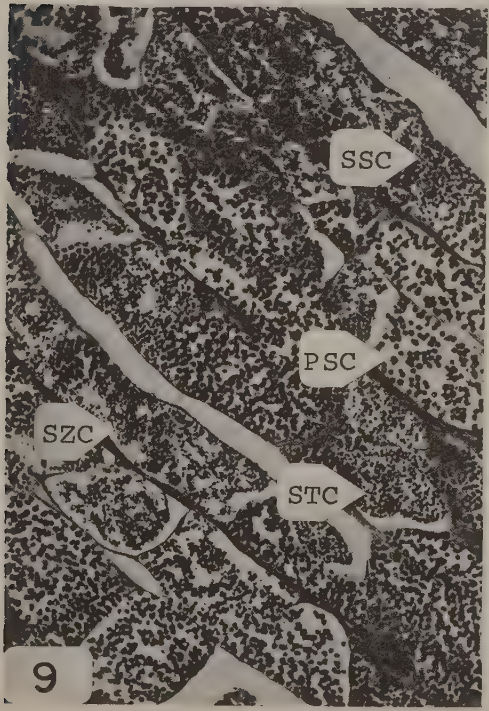
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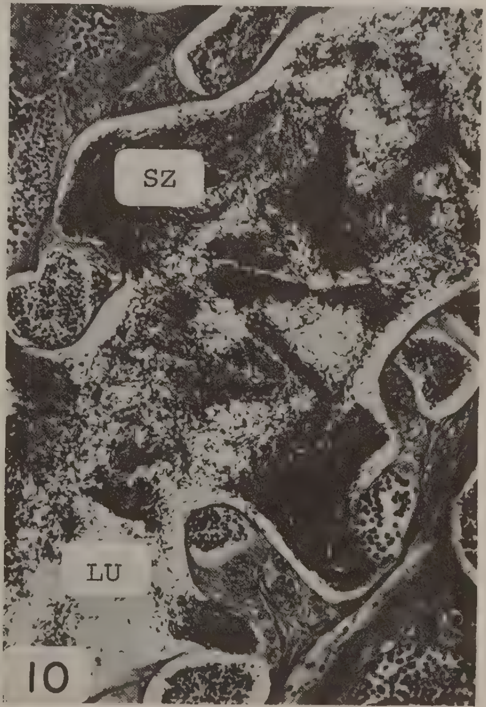
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PLATE 3

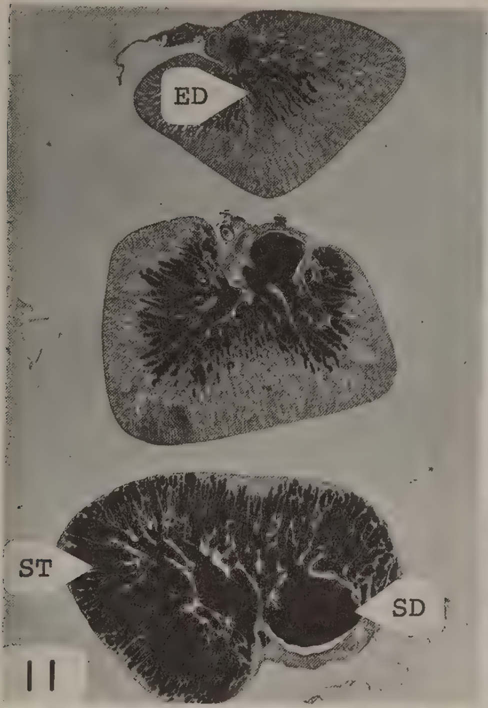
EXPLANATION OF FIGURES

11 Cross-sections of anterior (top), middle (center), and posterior (bottom) regions of testis of 445-mm *S. paucispinis* collected January 15, 1965. Spermatozoa fill only efferent ductules in anterior section but fill part of seminiferous tubules in middle section and fill tubules completely in posterior section. Masson's trichrome stain. 5.2 ×.

12 Fibrous tissue between blind ends of two seminiferous tubules in testis of 390-mm *S. paucispinis* collected September 12, 1964, showing migrating germ cells with dark elongate nuclei and clear cytoplasm. Masson's trichrome stain. 500 ×.

13 Cross-section of seminiferous tubule of 470-mm *S. paucispinis* collected December 14, 1964, showing dark PAS-positive granules at distal ends of tubule-boundary cells and the residual spermatozoa. 500 ×.

14 Frozen section of testis of 478-mm *S. paucispinis* collected January 18, 1964, showing dark sudanophilic granules in tubule-boundary cells. Sudan Black and hematoxylin. 125 ×.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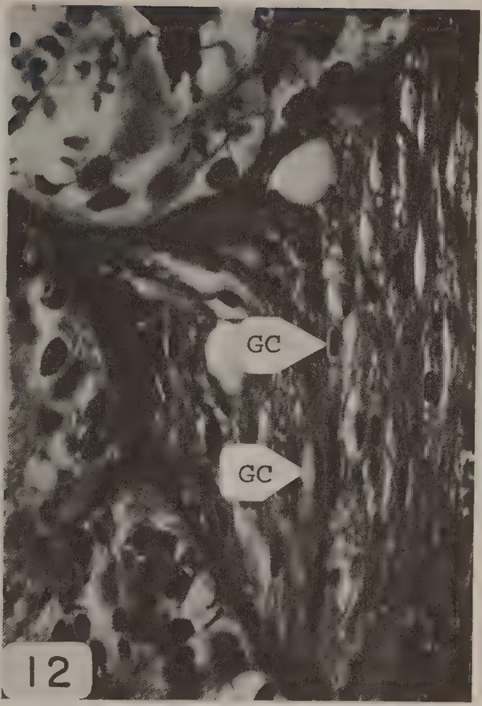
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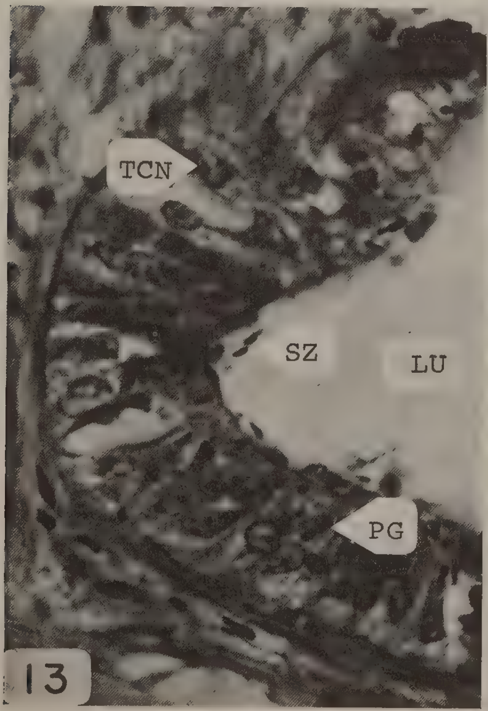
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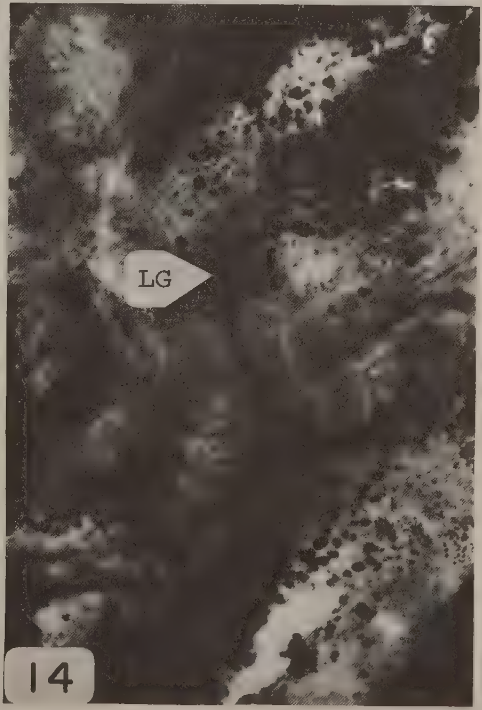
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PLATE 4

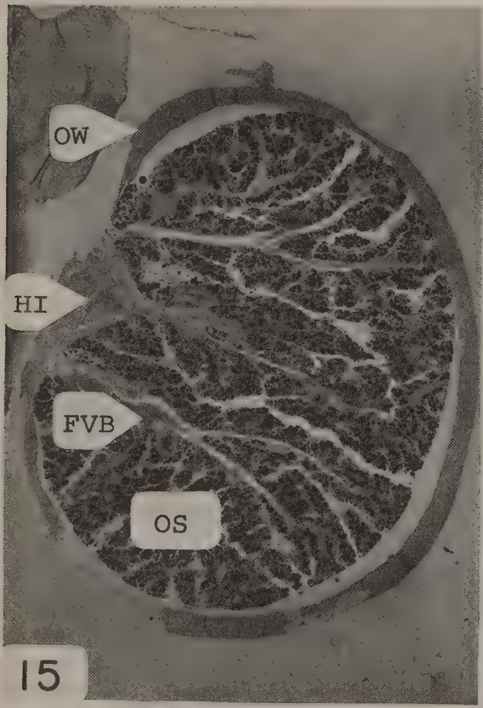
EXPLANATION OF FIGURES

15 Cross-section of spent ovary of 506-mm *S. paucispinis* collected March 21, 1964. Compact stroma is supported on fibrovascular branches attached to dorsal hilum. Numerous residual oocytes (less than 0.2 mm) appear throughout the stroma. Hematoxylin and eosin. 5.4 ×.

16 Section of ovarian wall of same specimen as in figure 15, showing inner longitudinal and outer circular layers of smooth muscle. Masson's trichrome stain. 125 ×.

17 Oogonial nest of same specimen as in figure 15, showing oogonia and oocytes in various maturational stages. Masson's trichrome stain. 500 ×.

18 Synapsis in oogonial nest of 433-mm *S. paucispinis* collected August 22, 1964. Masson's trichrome stain. 500 ×.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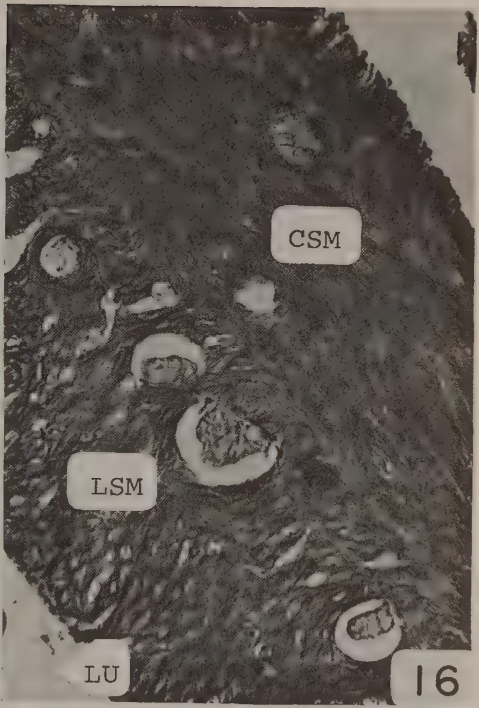
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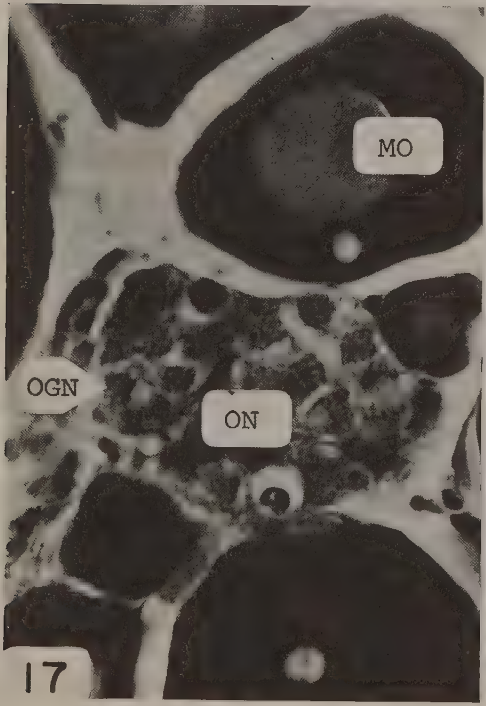
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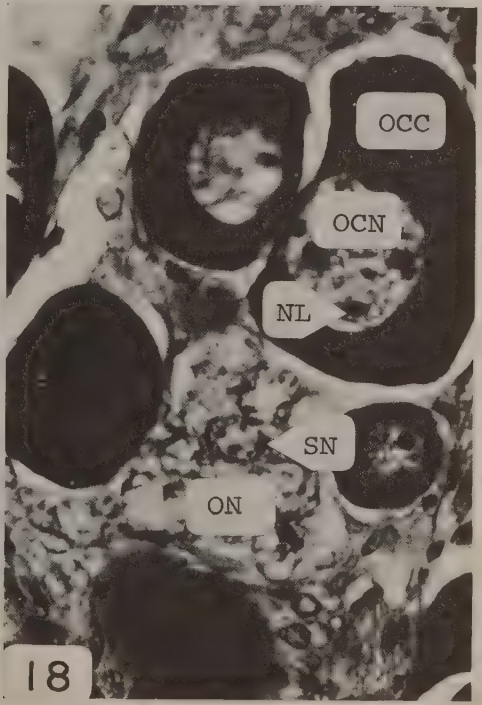
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PLATE 5

EXPLANATION OF FIGURES

19 Oogonial nest surrounded by maturing oocytes in ovary of same specimen as in figure 15. Masson's trichrome stain. 125 ×.

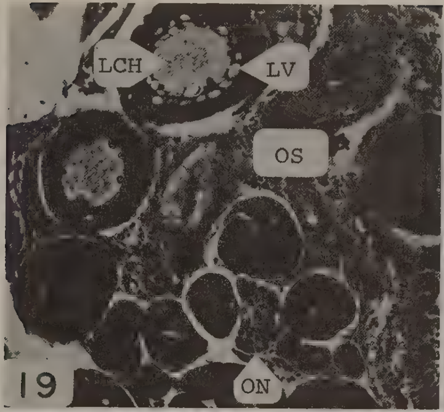
20 Section through maturing ovary of 510-mm *S. paucispinis* collected July 11, 1964. Zone of yolk globules is forming in large oocyte. Masson's trichrome stain. 125 ×.

21 Oocytes at a later stage of vitellogenesis in ovary of 511-mm *S. paucispinis* collected September 12, 1964, showing perinuclear zone of lipoid vesicles and wide zone of enlarged yolk globules. Masson's trichrome stain. 50 ×.

22 Nearly mature oocytes in ovary of 490-mm *S. paucispinis* collected October 17, 1964. The peripheral yolk globules are beginning to break down in some of the oocytes and the lipoid droplets are beginning to coalesce into larger droplets. Masson's trichrome stain. 50 ×.

23 Transverse section through follicles of two mature oocytes in ovary of 490-mm *S. paucispinis* collected October 17, 1964, showing bilaminar vitelline membrane with radial striations (pore canals). Masson's trichrome stain. 1250 ×.

24 Tangential section of mature oocyte of 450-mm *S. paucispinis* collected January 16, 1965, showing porous nature of vitelline membrane and a polar view of granulosa cells. Masson's trichrome stain. 500 ×.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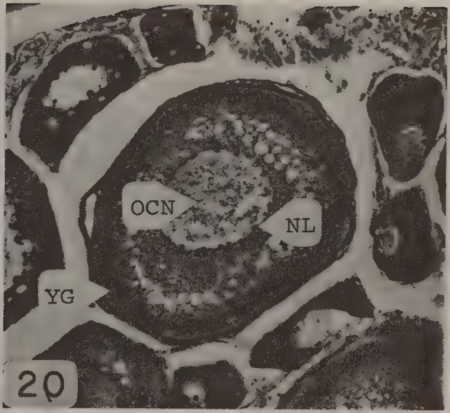
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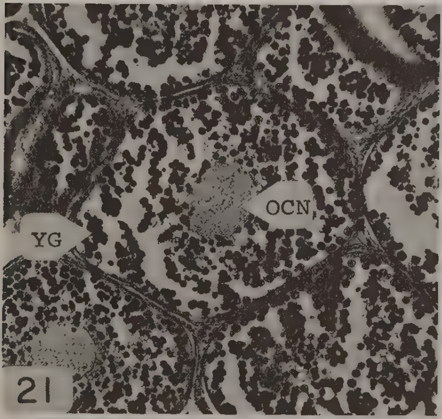
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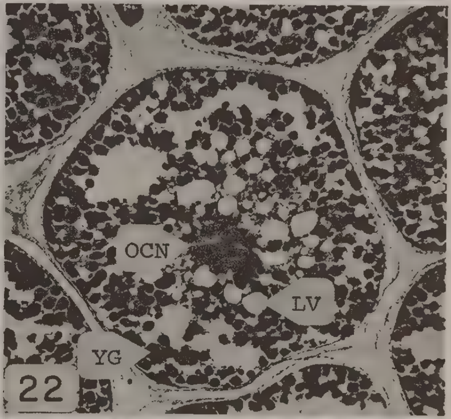
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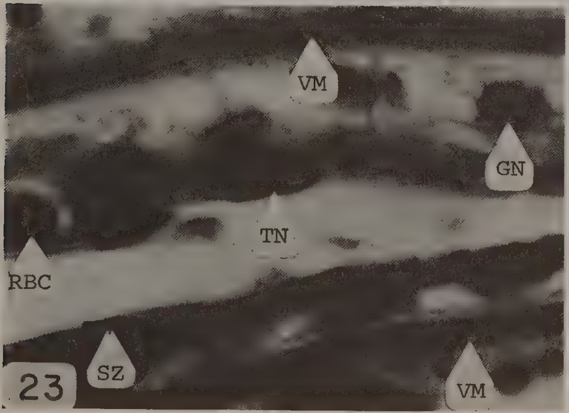
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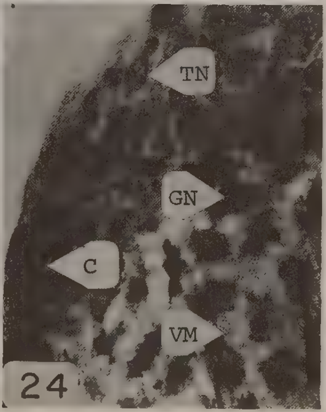
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PLATE 6

EXPLANATION OF FIGURES

25 Blastula surrounded by empty follicles in ovary of 380-mm *S. paucispinis* collected October 17, 1964. Masson's trichrome stain. 50 ×.

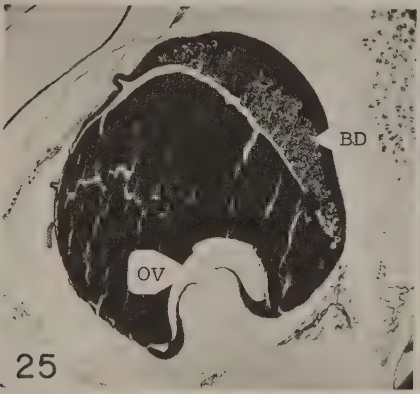
26 Empty follicle of first mode of oocytes next to oocyte of second mode in ovary of 452-mm *S. paucispinis* collected December 16, 1964, showing intact capillary containing erythrocytes and rounded condition of granulosa and theca nuclei. Masson's trichrome stain. 500 ×.

27 Unhatched prolarva of first brood in ovary of 380-mm *S. paucispinis* collected January 15, 1965. Maturing oocytes of second mode surround prolarva.

28 Atretic oocytes in ovary of 451-mm *S. paucispinis* collected January 14, 1964. Masson's trichrome stain. 50 ×.

29 "Pre-ovulatory corpus luteum" in ovary of 490-mm *S. paucispinis* collected October 17, 1964. Small yolk globules fill hypertrophied granulosa cells at periphery of oocyte and cluster of lipoid vesicles lies within amorphous yolk. Non-atretic oocytes surround "corpus luteum." Masson's trichrome stain. 125 ×.

30 Late-stage "corpus luteum" in ovary of 500-mm *S. paucispinis* collected March 21, 1964. Capillaries and granulosa nuclei have invaded remaining yolk which is mostly oil vesicles. Melanistic pigment is associated with oil vesicles. Masson's trichrome stain. 500 ×.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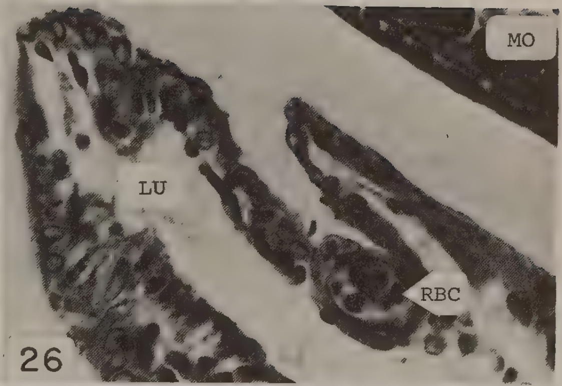
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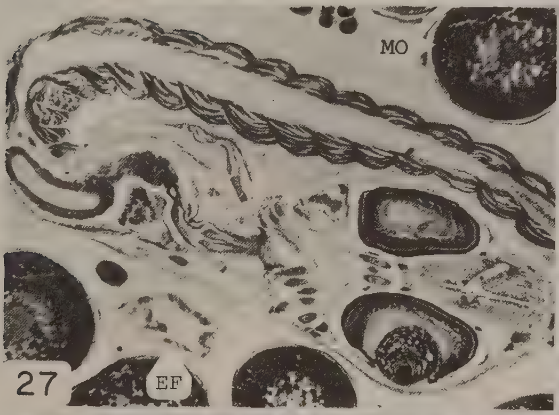
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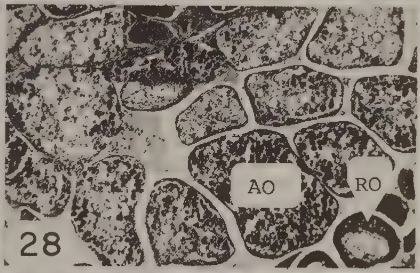
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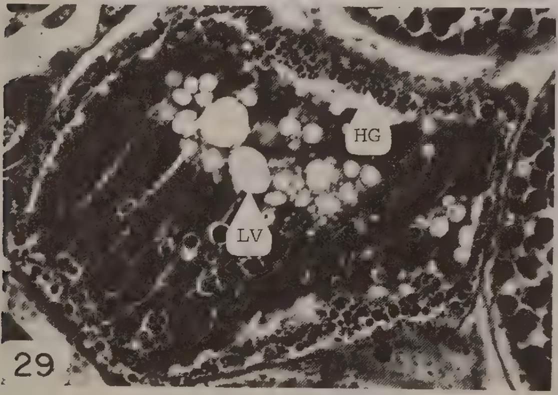
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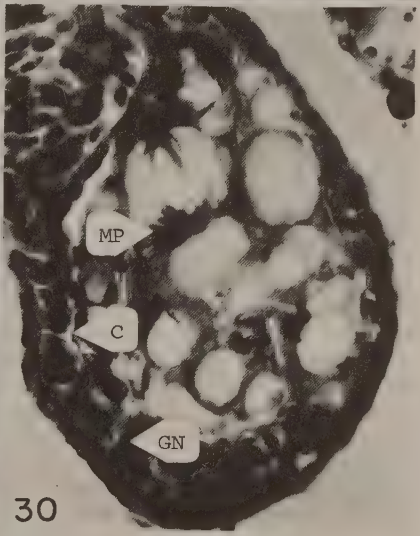
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SALMON OF THE NORTH PACIFIC OCEAN—PART VII
PINK SALMON IN OFFSHORE WATERS

by
Ferris Neave, Fisheries Research Board of Canada Biological Station,
Nanaimo, British Columbia, Canada
Teruo Ishida, Hokkaido Regional Fisheries Research Laboratory, Fisheries Agency,
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Seattle, Washington, U. S. A.

November 1965

CONTENTS

	Page
Introduction	1
Distribution of Spawning Stocks	1
Offshore Distribution	4
Horizontal distribution	4
Vertical distribution	5
Distribution and environment	5
Growth, Sex Ratio and Gonad Development	7
Identification of Area of Origin of Pink Salmon Occurring in Offshore Waters	8
Evidence from tagging	8
Evidence from scales, meristic and non-meristic characters	18
Evidence from other sources	31
Mingling of Stocks in Offshore Waters	35
Literature Cited	37

INTRODUCTION

The pink salmon (*Oncorhynchus gorbuscha* Walbaum) on the average provides a larger portion of the total annual catch of Pacific salmon than any other single species. During the 8-year period from 1954 to 1961 it contributed about 40 percent of the weight and nearly 60 percent of the number of all salmon caught commercially in the North Pacific and adjacent seas and fresh waters. During the same period this species constituted about 50 percent by weight of the total salmon catches made on the high seas (mothership *plus* offshore landbased catches), although only about 25 percent of the mothership catch alone (Kasahara, 1963).

Information on the historical development of the offshore pink salmon fisheries and on the progress of biological studies prior to the initiation of the extensive cooperative research program of the International North Pacific Fisheries Commission (INPFC) in 1955 is provided by Kubo *et al.* (1955), Hirano (1953), Taguchi (1957, 1962), Kasahara (1961, 1963), Pravdin (1940), Barnaby (1952), Schaeffers and Fukuhara (1954) and others.

The present account deals mainly with comparatively recent work on the identification of the origin of pink salmon caught on the high seas and with the resultant conclusions on the offshore distribution and movements of fish originating in different parts of the vast region inhabited by the species. Investigation of these matters is continuing. A review such as this, which has necessitated the exchange and consideration of information by widely separated agencies, inevitably fails to harvest the latest crop of findings. In preparing the following pages the results of investigations made up to the end of 1962 have been examined. A few references are made to later findings when these are of special significance.

DISTRIBUTION OF SPAWNING STOCKS

The geographical distribution of pink salmon spawning streams in Asia extends from the Tumen and North Nandai Rivers of North Korea and the Japanese island of Hokkaido northward along the mainland coast and islands to the Yana and Lena Rivers which flow into the Arctic Ocean. On the North American side occasional occurrences of pink salmon are noted in the Russian River of central California and the rivers of Oregon. Regular spawning extends from the Puyallup River in the State of Washington northward to central Alaska, westward to Attu Island, northward to northern Alaska and eastward to the Mackenzie River in the Northwest Territories, Canada (Fig. 1).

Throughout this vast region the invasion of coastal areas by maturing pink salmon occurs mostly within the seasonal period of June to September, inclusive. Entrance into fresh water takes place from July to October, and is followed rather closely by spawning.

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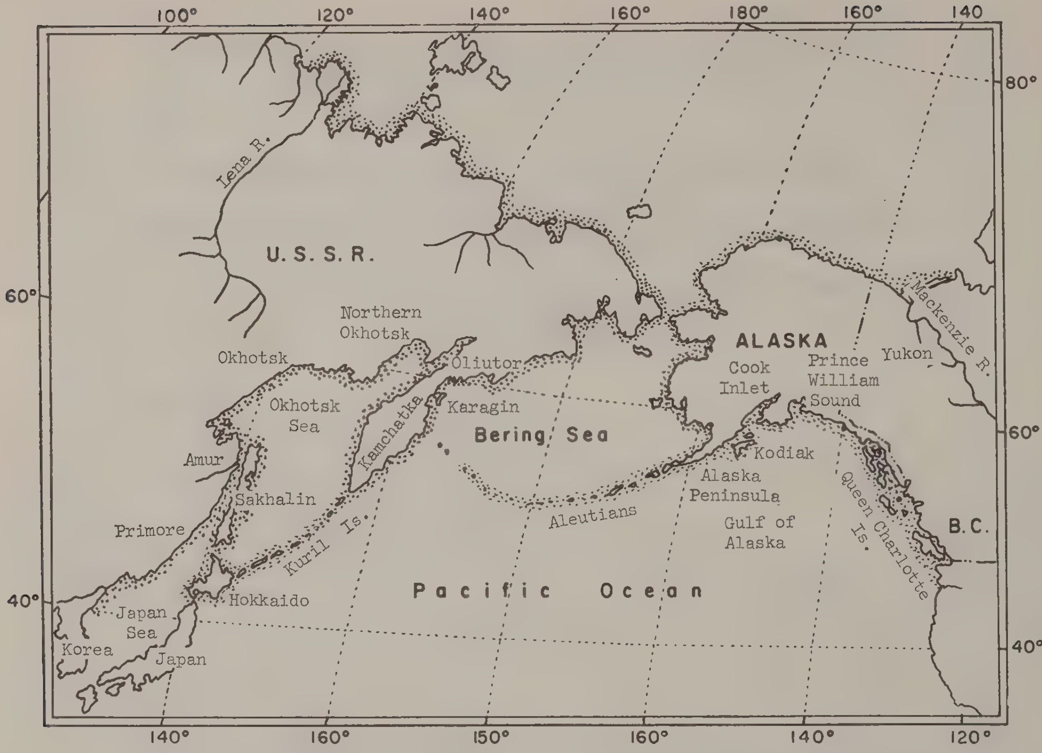
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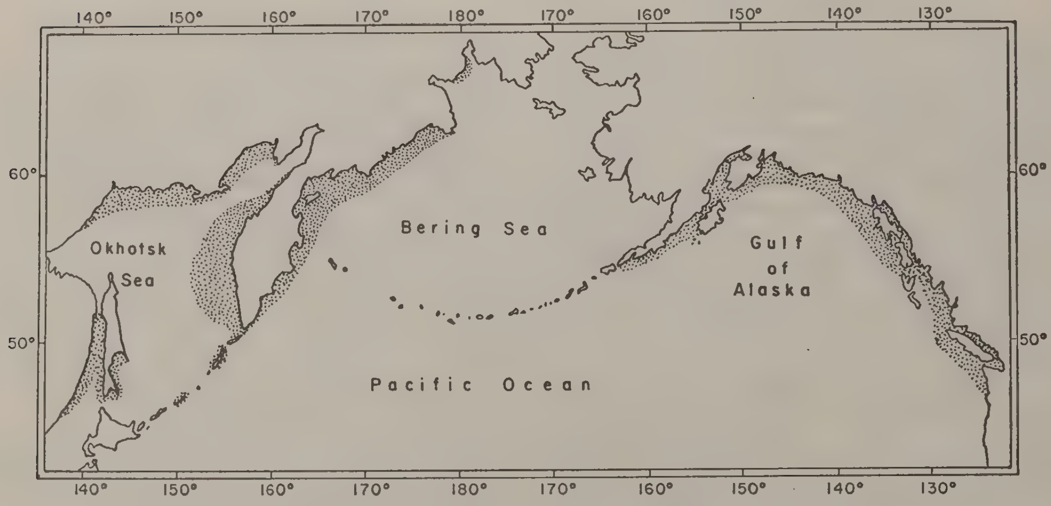
Lena R.
U.S.S.R.
Northern Okhotsk
Okhotsk
Oliutor
Okhotsk Sea
Kamchatka
Karagin
Bering Sea
Amur
Sakhalin
Primore
Kuril Is.
Hokkaido
Japan Sea
Korea
Japan
Aleutians
ALASKA
Cook Inlet
Prince William Sound
Yukon
Mackenzie R.
Kodiak
Alaska Peninsula
Gulf of Alaska
Queen Charlotte Is.
B.C.
Pacific Ocean

Figure 1. North Pacific region, showing general coastal distribution of pink salmon (stippling).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130°
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50°
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Okhotsk Sea
Bering Sea
Gulf of Alaska
Pacific Ocean

Figure 2. General distribution of important spawning areas in odd-numbered years. Stippled areas indicate roughly the relative sizes of spawning populations.

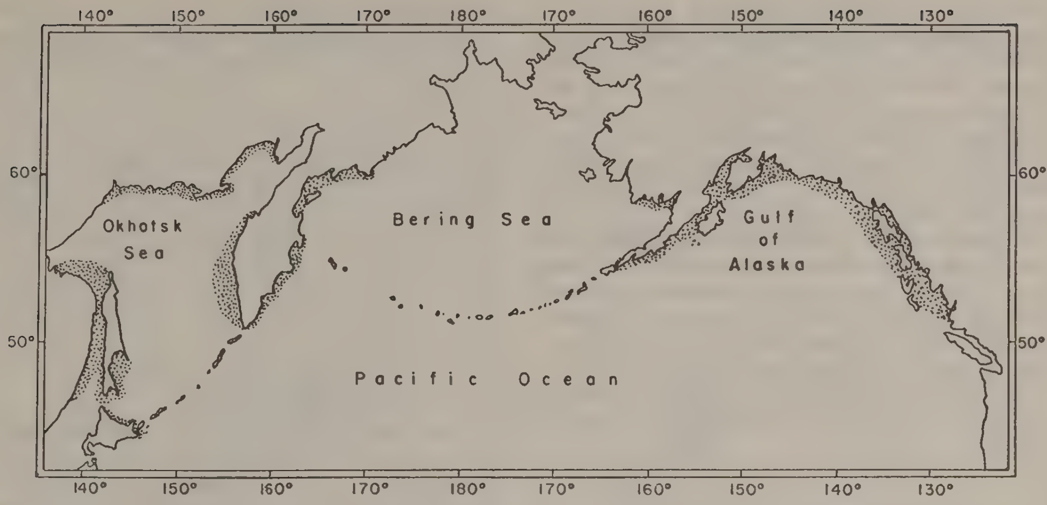

FIGURE 3. General distribution of important spawning areas in even-numbered years. Stippled areas indicate roughly the relative sizes of spawning populations.

The timing of any particular run is considerably more restricted than is indicated by the above inclusive statements. Information on the timing of runs in different areas is given by Ishida (MS 1964, 1966) ; Neave (1966) ; Aro and Shepard (MS 1966) ; Atkinson *et al.* (MS 1966).

In assessing the relative importance of different areas in the production of pink salmon, peculiarities resulting from the 2-year life cycle which is normal for the species must be taken into account. As is well known (and discussed in other parts of this report and elsewhere) the populations of any two consecutive years are genetically segregated from each other and sometimes differ greatly in abundance. In extreme cases a coastal area may have large numbers of pink salmon at regular 2-year intervals and almost none in the intervening years. Much information on the relative abundance of " even-year " and " odd-year " populations in different parts of the geographic range of the species, and on the occasional shifting of numerical dominance from one line to the other, has been given by Ricker (1962). Data on the annual catches made in the various regions in which pink salmon are fished are given by Kasahara (1963). Figures 2 and 3, and the following brief notes, indicate certain broad features in the pattern of distribution.

Only a very small number of pink salmon spawn in the streams of North Korea. In Primore, pink salmon runs of commercial importance occur only in the northern part. The region has not shown consistent large differences between even- and odd-year catches. There are no important pink salmon spawning streams along the southern part of the Japan Sea coast of South Sakhalin. The Teshio River in northern Hokkaido is considered to be the southernmost limit of spawning grounds along the Japan Sea coast of Hokkaido.

The Yurappu River is the southernmost limit of pink salmon spawning on the Pacific Ocean side of Hokkaido. The Tokachi River and streams farther eastward along this coast are still visited by pink salmon.

North of the Japan Sea the Amur River system provides spawning grounds for very large stocks of pink salmon in even years. Throughout most of the recorded history of the fishery the odd-year stocks have shown a much lower level of abundance.

Other important pink salmon streams are distributed along the coasts of the Okhotsk Sea —in northwestern and eastern Sakhalin, the Okhotsk and northern Okhotsk coasts, West Kamchatka and the Kuril Islands.

East Kamchatka, bordering the North Pacific Ocean and the Bering Sea, has very important pink salmon spawning streams, especially in the Karaginskii and Oliutorskii areas. The number and importance of spawning streams decreases northward from this region.

Throughout the Okhotsk Sea and East Kamchatka regions odd-year populations have tended to be dominant in recent years.

On the North American side very little information is available for northern Alaska and the Northwest Territories but the runs to these regions are not considered large.

Runs of some importance occur in even years in Bristol Bay. Large annual runs appear on the northern and western coasts of the Gulf of Alaska (Alaska Peninsula, Kodiak Island, Cook Inlet and Prince William Sound). The runs to southeastern Alaska are of roughly equivalent magnitude to those of the northern and western coasts of the Gulf of Alaska, and do not show consistent differences between even and odd years.

In northern and central British Columbia as a whole, runs of considerable size occur in all years. However, a small area in the Queen Charlotte Islands has produced only even-year spawnings throughout recorded history. At the southern end of the province, and in the adjacent Puget Sound area of the United States, large odd-year populations alternate with years in which the number of pink salmon is negligible.

OFFSHORE DISTRIBUTION

Knowledge of the distribution of pink salmon in the international waters of the North Pacific has increased immensely (although limited mainly to the spring and summer seasons) as a result of (1) the Japanese mothership driftnet fishery which started in 1952, (2) the Japanese landbased driftnet and longline fishery which expanded at about the same time and (3) the large-scale cooperative investigations begun in 1955 by the three member nations of the INPFC—Japan, the United States and Canada. The information now available, together with the large amount of data that served as the basis, is summarized in Part V of *Salmon of the North Pacific Ocean* (Manzer *et al.*, 1965), wherein the distribution of salmon in the high seas has been analyzed from catch records using the catch-per-unit-effort (CPUE) of the gillnet catch by fishery and research vessels as the index of relative density. Fortunately, the mesh size, thread and other specifications of the nets used in the high seas fisheries of Japan were almost the same between the years 1956 and 1960, and the gillnets used by the research vessels have been standardized in the research programs of INPFC since 1957. However, it cannot be assumed that the CPUE and the true density are always related by a constant factor in view of the fact that salmon gillnets ordinarily catch fish only within six meters of the surface. In other words, we have only a limited knowledge as yet regarding the degree to which the CPUE may be affected by such possibilities as differences in the swimming depth and in the direction and speed of migration associated with age, season or area.

Horizontal Distribution

Most of the high seas fishing and research vessel operations have started in May. The fish which are encountered at this season have been in the sea for about a year and appear to have already begun to move in the general direction of their spawning areas. According to Manzer *et al.* (1965, p. 98–99), "... In general, in May, pink salmon occurred in a continuous wide band across the North Pacific. The width of this band in the western Pacific extended roughly between northern Honshu in the south to about Latitude 52°N in the north. Approximate corresponding southern and northern limits in the eastern Pacific were Latitudes 45°N to 55°N, respectively." (Fig. 4). These limits exclude the Bering Sea and a northwestern portion of the Gulf of Alaska. However, the northern and southern boundaries and the density of pink salmon distribution in May have not been determined as accurately as for the following months because the regional coverage in May has been small and because the small size of the fish makes them difficult to catch with gillnets. In addition, as noted earlier, it is highly possible that the CPUE during this period is not directly proportional to the true density in view of the habits of the fish. As an example, in the Pacific Ocean off the southern Kuril Islands a large number of pinks are caught by longlines operated during this period, but hardly any are caught by gillnets (personal communication from Satoru Nakamura, Kushiro Branch, Hokkaido Prefectural Fisheries Experimental Station). In any case, the CPUE values, as can be seen in Figure 4, are mostly low, being medium only in the waters of the southern Kurils and south of the Aleutians.

In June, "... pink salmon did not occur as far south as in May, and in addition were present in the northern Gulf of Alaska and in the Bering Sea as far north as fishing was conducted (Latitude 60°N)" (*loc. cit.*). In this month the catch by gillnets rapidly increases in some areas. Large differences have been found in the relative densities of pink salmon between the odd years and the even years in some high seas areas. Thus, "... In odd-numbered years, especially in June, pink salmon were very abundant in the North Pacific from the Kurils eastward to the eastern Aleutians and into the central areas of the Bering Sea. They were considerably less numerous in the eastern areas of the Bering Sea, in southern waters of the central North Pacific and in the Gulf of Alaska" (*loc. cit.*). On the other hand, "... In even-numbered years in June, pink salmon were concentrated in the western Pacific but, in contrast to the distribution pattern in odd-numbered years, this concentration did not extend eastward much beyond

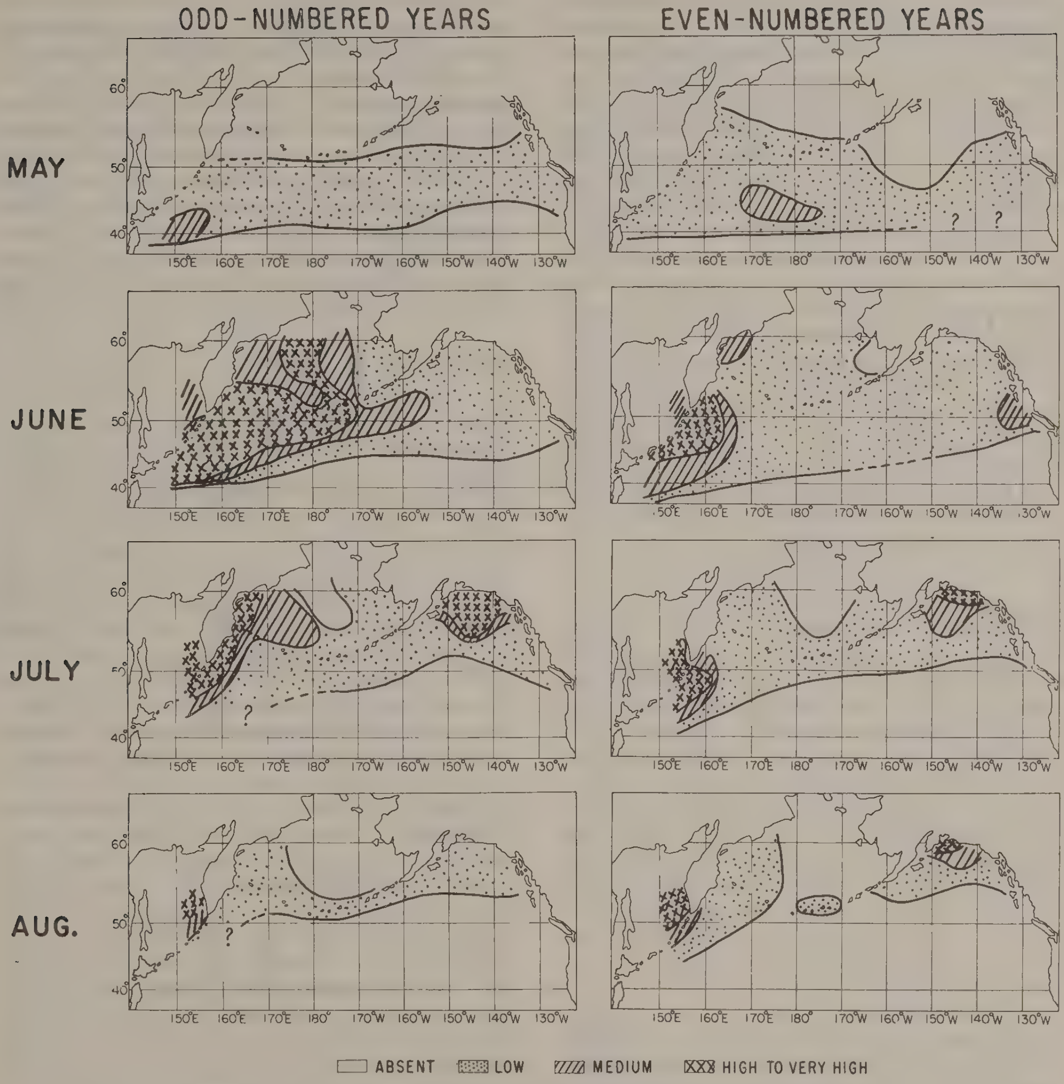
ODD-NUMBERED YEARS
EVEN-NUMBERED YEARS
MAY
JUNE
JULY
AUG.
60°
50°
40°
150°E 160°E 170°E 180° 170°W 160°W 150°W 140°W 130°W
?
ABSENT
LOW
MEDIUM
HIGH TO VERY HIGH

Figure 4. Schematic diagram showing distribution and relative abundance of pink salmon in odd- and even-numbered years, May through August (from Manzer *et al.*, 1965, Fig. 29).

Abundance level	*Mothership catch/tan*	*Research vessel weighted catch*/3000 ft
low	0.1–1.0	1–10
medium	1.1–2.0	11–20
high	2.1–3.0	21–30
very high	over 3.0	over 30

Longitude 170°E. Also differing from the distribution pattern of odd-year pink salmon, a minor area of concentration of even-year pink salmon was suggested for the southeast Gulf of Alaska " (*loc. cit.*). In the Okhotsk Sea off the northern Kurils and the Kamchatka Peninsula, the density of pink salmon in both even and odd years begins to rise at the beginning of June and becomes high to very high during late June and July.

In July, pink salmon in the high seas of the North Pacific Ocean are mainly concentrated near the coastlines and the total north-south limits of the distribution pattern become narrower. In odd-numbered years the densities of pink salmon were high to very high on both the east and west sides of the Kamchatka Peninsula, including the Oliutorskii and Karaginskii areas, and throughout the entire northern part of the Gulf of Alaska. In even-numbered years the densities were low in the high seas off the eastern coast of the Kamchatka Peninsula except for the southern part, and the distribution of high densities in the Gulf of Alaska was much more restricted than in odd-numbered years.

In August, with the departure of most of the fish to coastal and inland waters, the high seas distribution of pink salmon is limited to a narrow strip along the Aleutian chain and the waters near the spawning areas and the relative densities become generally low.

Certain differences in the timing of the movement towards shore from distant high seas areas have been noted in different years. For example, the peak of the pink salmon migration to the offshore areas of West Kamchatka in the Okhotsk Sea came in July in the years 1955 to 1957 but was in late June in the year 1958. Again, in the Aleutians and in the central Bering Sea regions, the peak of the migration in the year 1959 came about half a month later than in 1957.

VERTICAL DISTRIBUTION

As indicated previously, information on the high seas distribution of pink salmon has been derived almost entirely from surface fishing or by the use of gear (purse seine) which does not yield precise data on the depths occupied by the fish. In the Gulf of Alaska, in May-July, 1959 and 1960, a gillnet approximately 12 meters deep was suspended at various depths. At each setting, the net occupied one of the following depth intervals: 0–12 m; 12–24 m; 24–37 m; 37–49 m; 49–61 m. Details of sets and catches are given by Manzer (1964). In June 1961, at various stations in the Bering Sea, a Japanese research vessel used gillnets which occupied the following depth intervals: 0–6 m; 10–16 m; 20–26 m; 30–36 m; 40–46 m (INPFC, 1963). In June 1962, in three areas off the east coast of Kamchatka, sets were made covering: 0–10 m; 10–20 m; 20–30 m; 30–40 m; 40–50 m (INPFC, 1964a).

These experiments were carried out at places or times at which pink salmon were scarce. Irrespective of depth, many sets produced no individuals of this species. While it can be stated that no pinks were taken at depths greater than 24–37 m in the Gulf of Alaska, or 30–36 m in the Bering Sea, the data are too meager to provide conclusions on the total depth range inhabited or on diurnal or seasonal changes in the levels occupied.

DISTRIBUTION AND ENVIRONMENT

In spite of the limited time spent in the sea, the total ocean distribution of pink salmon is very extensive, as has been noted in previous paragraphs. One-way journeys by individual fish of 1,000 miles (1600 km) and even 1,700 miles (2700 km) have been recorded. The distribution, however, is not random. The influence of environmental conditions can be inferred from (a) the existence of a rather definite southern limit of distribution (known best for the spring and summer months) and of a northern limit in winter and early spring, (b) seasonal movements which do not seem to be a necessary part of spawning migrations and (c) differences between the ocean distribution of pink salmon and that of other species which breed in the same areas and enter the sea at about the same time of year.

A relationship between water temperature and availability of pink salmon has long been accepted by Japanese fishermen and investigators. In the earlier months of the year, pink salmon of both Asian and American origin are mostly well to the south of their breeding areas. None were found in exploratory fishing operations in the Bering Sea in February 1963, and a similar absence of pinks has been noted in the northwestern Gulf of Alaska in April and May (sockeyes were present in at least parts of these regions). Later in the season pink salmon are numerous in these areas.

This seasonal northward or northwestward movement, while it tends to bring the fish nearer to their spawning areas, is not necessarily a purely " spawning migration " in a strict sense. Similar movements at the same season are made by many strictly marine fishes such as the pomfret (*Brama raii*), blue shark (*Prionace glauca*), jack mackerel (*Trachurus symmetricus*), and albacore (*Thunnus alalunga*) (Neave and Hanavan, 1960). In other species of Pacific salmon (with a longer period of ocean residence) such movements are made by immature as well as by maturing fish. Moreover, as favorable temperatures extend northward, pink salmon belonging to the more southerly spawning populations of both Asia and America frequently migrate beyond the latitude of their ultimate destination, the final approach to fresh water thus being made from the north. Feeding and growth continue throughout the migrations, the fish thereby exploiting ocean regions which are avoided in the colder months.

Data and discussion of high seas catches of pink salmon in relation to temperature are given by Manzer *et al.* (1965). Reference is also made to Kaganovski (1949), Hirano (1953), and Taguchi (1957).

Although small numbers of pink salmon have sometimes been caught in ocean water temperatures as low as 3°C, they are seldom abundant when surface temperatures are less than 5°, while 6° to 9° is considered to be a favorable range. In high seas fishing in early and mid-summer, pink salmon are mainly caught in waters not warmer than 12°. In general conformity with this isotherm, the southern boundary of the high seas distribution of the species in early spring (April, May) lies at about 40°N off the Asian coast and about 45°N near the American coast. The southern limit of recorded catches shifts northward with the progress of the season. In late summer, however, in the coastal stages of their migration to the spawning streams, pink salmon sometimes occur in waters with surface temperatures as high as 14° or 15°C.

The opinion has been expressed (e.g., by Kaganovski, 1949 ; Semko, 1958) that the distribution and migration routes of salmon in the ocean are influenced by the abundance of food organisms. Boundary areas between warm and cold currents in the western Pacific have been thought to provide particularly rich feeding grounds.

Examination of many stomachs of ocean-caught pink salmon has shown that the diet, at least in summer, consists mainly of organisms which can be placed in the following categories : fish, euphausiids, amphipods, crustacean larvae, copepods, squid and pteropods. The relative importance of these categories varies widely from place to place and from time to time. Andrievskaia (1957) found that, in the western Pacific (between southern Kamchatka and 172°E) in June and July 1955, fish constituted the largest item (by weight), followed by euphausiids and amphipods.

Allen and Aron (1958) also reported on the stomach contents of pink salmon caught in the spring and summer of 1955 in the western Pacific and in the Okhotsk Sea. In regions off both the west and east coasts of Kamchatka, amphipods ranked first (in volume), followed by fish and crustacean larvae. In a region farther east (about 48°–50°N, 165°–172°E) the ranking was (1) copepods, (2) euphausiids, (3) fish, (4) amphipods.

In the stomachs of pink salmon collected in the Gulf of Alaska during three years, the rankings of categories constituting 10 percent or more of the volume were : 1956 (June, July) : (1) euphausiids, (2) squid, (3) fish ; 1957 (May-August) : (1) euphausiids, (2) squid, (3) copepods, (4) amphipods, (5) fish ; 1958 (May-July) : (1) fish, (2) euphausiids, (3) amphipods, (4) crustacean larvae (Neave and Manzer, 1957 ; Manzer and Neave, 1958, 1959).

While it is reasonable to suppose that the distribution and movements of pink salmon are influenced by the availability of food organisms, there are as yet insufficient data to chart such a relationship. Evidently the fish in their total feeding habits are not restricted to a narrow range of organisms. On the other hand, the contents of individual fish often consist almost entirely of a single kind of food or, in other instances, of two kinds occupying separate regions of the stomach. This suggests that the salmon were feeding quite selectively or that they were feeding only at times and places at which a particular kind of food was dominant. To determine the favorability or otherwise of the environment from the standpoint of food supplies requires not only quantitative data on the total abundance of potential food organisms in an area, but also information on the selection practiced by the fish and on the availability of the various organisms at different stages of their daily vertical migrations. Finally, it is noted that the ocean distribution of pink salmon differs from that of sockeye, although the latter species feeds largely on the same kinds of organisms.

GROWTH, SEX RATIO AND GONAD DEVELOPMENT

Pink salmon enter the sea at about 3.5 cm fork length (0.2 g live weight) and are usually 40–60 cm long (1.5–2.5 kg in weight) at the time of their return to fresh water. Feeding and growth continue, at least to some extent, and gonad weight increases rapidly during the shoreward migration.

The average fork length of pink salmon in the northwestern Pacific Ocean in May (Table 1) is in general about 40 cm and becomes about 50 cm in August (Manzer *et al.*, 1965). These figures, however, were obtained by sampling fish from a wide area in several different years and hence do not necessarily represent the growth of any particular stock or year class.

In the eastern Gulf of Alaska in 1962, pink salmon

TABLE 1. Estimated average fork lengths (cm) and sex ratios (percentage male) of pink salmon in the available populations in the mothership and landbased regions[1].

Fork length		May	June	July	August
Mothership	Female	42	44	46	50
1957–1960	Male	44	45	47	51
Landbased	Female	39	43	47	52
1957–1960	Male	41	44	47	53
Sex ratio (percentage male)					
Mothership					
1957–1960		92	75	53	44
Landbased					
1957–1960		60	52	43	47

[1] from Manzer *et al.* (1965).

which were considered to be of central British Columbian origin grew from a fork length of about 35 cm in April to 49 cm in late July, as determined from longline catches in the areas through which these fish migrated. Relatively rapid growth in the early part of this period was followed by a slower increase in length in July. Some growth, however, appeared to continue even after the fish had left the high seas and had entered the coastal fishery. A detailed examination of data relating to the growth in length and weight of pink salmon of this stock, and a compilation of recorded measurements from other areas, are contained in a recent paper by LeBrasseur and Parker (1964).

The sex ratio of pink salmon caught in the western high seas varied greatly from month to month even when a correction was made for the selectivity of gillnets in relation to the different size of males and females. As is shown in Table 1, in both the mothership and the landbased fishery areas the number of males was extremely high in the beginning but decreased as the season progressed, the females becoming dominant in July and August. When the mothership and the landbased fishery areas are compared, males were dominant until later in the season in the former. One of the reasons for such a difference in sex ratio might be a difference in the time when the males and females start their spawning migration. If, however, the segregation of sexes is real, the question remains as to where the females were located at the time the males were dominant. In samples taken by longline in the eastern Gulf of Alaska from early April to late July 1962, no consistent differences in sex ratio were found.

The gonads of pink salmon show rapid growth in the later stages of marine life. According to Ishida and Miyaguchi (1958), the gonad weights of pink salmon caught by motherships were less than 20 g for females and less than 5 g for males in early and late May; 10 to 60 g for females and about 10 g for males in early June; the median value for females was 75 g and between 10 and 100 g for males in mid to late July. The frequency distribution for both males and females was skewed toward the smaller weights. Unpublished data from the eastern Gulf of Alaska (for 1962) indicated that gonad weight relative to body weight increased rapidly from April onward for males and from May onward for females.

IDENTIFICATION OF AREAS OF ORIGIN OF PINK SALMON OCCURRING IN OFFSHORE WATERS

EVIDENCE FROM TAGGING

Discussion

Tagging experiments, when successful, provide positive evidence of the movement of individual fish from the points at which they are released to the points at which they are recaptured. Strictly speaking, therefore, tag recoveries show destinations (final or intermediate) rather than places of origin. Since there is ample evidence of the very strong tendency of Pacific salmon to return to their natal watersheds for spawning, it is customary to assume that areas of origin and of final destination are identical. While this is an entirely reasonable assumption when a consistent pattern is shown by tag returns, the possibility of " straying " cannot be entirely dismissed in the case of an isolated recovery unsupported by other evidence.

Assuming the general applicability of the homing tendency, tagging is well adapted to indicating the occurrence of regional stocks at the place and time of the tagging operation. Quantitative comparisons between the stocks represented are difficult because of differences in fishing intensity and efficiency of tag recovery in coastal areas and the possibility that mortality due to tagging increases with the time elapsing between tagging and recovery. Further, in view of the long coastwise journeys that are known to be made by pink salmon in certain regions, the recovery near shore of an individual tagged on the high seas does not *ipso facto* prove that it was near its final destination. For example, pink salmon tagged on the south side of the Alaska Peninsula and others tagged at the south end of the Queen Charlotte Islands (on the outer British Columbia coast) have been recovered several hundred miles north of the tagging points. In both instances the fish had probably migrated from distant high seas localities before being intercepted by the taggers. Fortunately, much commercial fishing is conducted sufficiently close to the spawning streams to justify a belief that the fish caught are not proceeding to far distant regions.

While tagging can provide information on the racial composition of fish at the tagging point, operations must be conducted at many different places and times in order to reveal the manner in which a given population is deployed in the ocean. In addition to many other considerations, it is evidently necessary to tag large numbers of fish, since the percentage of recoveries from high seas tagging operations has always been

TABLE 2. Pink salmon tagged in high seas investigations, 1956–1962.

Year	Tagging country	Region	Period	Gear[1]	Kind of tag[2]	Number tagged	Number recovered			Reference
							Coast	High seas	Total	
1956	U.S.	Aleutian	May–Aug.	P	d,t	146	0	1	1	Hartt (1962)
	U.S.	Gulf of Alaska	Sept.	P	d,t	93	0	0	0	»
1957	U.S.	Aleutian	June–Aug.	P	d,t	6,319	50	19	69	Hartt (1962)
	Japan (W. Pac. (C. Pac.	Aleutian Bering Sea	May–July	G	A,t	148	0	1	1	INPFC (1958)
1958	U.S.	Aleutian	May–Aug.	P	d,t	282	4	2	6	Hartt (1962)
	U.S.	Bering Sea	May–Aug.	P	d,t	32	1	0	1	»
	U.S.	Gulf of Alaska	June–Sept.	P	d,t	23	2	0	2	»
						219[3]	0	0	0	
	Japan	Aleutian	June	L	t	62	1	0	1	INPFC (1959, 1960)
	Japan	W. Pacific	June–Aug.	L	t	184	0	44	44	»
1959	U.S.	Aleutian	May–Aug.	P	d	2,719	37	114	151	Fish. Res. Inst (1960a, b)
	U.S.	Bering Sea	June, July	P	d	146	0	13	13	»
	U.S.	Gulf of Alaska	May	P	d	4	0	0	0	»
	Japan	Aleutian	June, July	L	t	502	1	6	7	Fish. Ag. Jap. (1960 a, b)
	Japan	W. Pacific	May-August	L	t	700	8	16	24	»
	Japan	C. Pacific	June	L	t	121	0	0	0	»
	Japan	Bering Sea	July	L	t	679	11	18	29	»
1960	U.S.	Aleutian	May–Aug.	P	d	1,322	17	31	48	Fish. Res. Inst. (1961)
	U.S.	Gulf of Alaska	April	P	d	3	0	0	0	»
	Japan	Aleutian	June	L	d	8	0	0	0	Fish. Ag. Jap. (1960 c, 1961 a, b, c)
	Japan	W. Pacific	May–July	L	d,t	2,329	5	50	55	»
	Japan	C. Pacific	May, June	L	d	160	0	1	1	»
	Japan	Bering Sea	June, Aug.	L	d	26	1	0	1	»
1961	U.S.	Aleutian	June–Aug.	P	d	2,190	21	3	24	Fish. Res. Inst. (1962)
	U.S.	Gulf of Alaska	May–Sept.	P	d	1,542	249	0	249	»
					t	396[3]	1	0	1	»
	Japan	W. Pacific	Apr.-July	L	d	2,324	8	58	66	Fish. Ag. Jap. (1962 a, b, c)
	Japan	Bering Sea	June, Aug.	L	d	9	0	0	0	»
	Japan	C. Pacific	May	L	d	23	0	0	0	»
	Japan	Gulf of Alaska	Apr., May	L	d	59	1	0	1	»
	Canada	Gulf of Alaska	June-Aug.	L	d	441	26	0	26	INPFC (1963)
1962	U.S.	Aleutian	May-Aug.	P	d	312	17	0	17	INPFC (1964 a)
	U.S.	Gulf of Alaska	May-July	P	d	2,665	318	0	318	»
	Japan	W. Pacific	Apr.-Aug.	L	d	4,719	1	119	120	Fish. Ag. Jap. (1962 c, d, and suppl.), INPFC (1964 a)
	Japan	Okhotsk	May-Aug.	L	d	113	2	0	2	»
	Japan	C. Pacific	Apr.-June	L	d	416	0	1	1	»
	Japan	Bering Sea	Aug.	L	d	1	0	0	0	»
	Japan	Gulf of Alaska	May	L	d	31	0	0	0	»
	Canada	Gulf of Alaska	Apr.-July	L	d	7,929	548	0	548	INPFC (1964 a)

[1] G=Gillnet, L=Longline, P=Purse seine.

[2] A=Atkins, d=disc, t=tube.

[3] Juvenile fish.

relatively small (see Table 2).

In spite of these qualifications and limitations the extensive tagging experiments conducted within the framework of the INPFC research program have contributed in an outstanding way to knowledge of the ocean distribution of major pink salmon stocks.

Many years before the commencement of the INPFC research program, tagging experiments had demonstrated that pink salmon make long journeys in the ocean and that they pass at times from one major body of ocean water to another. For example, fish were recovered near the town of Okhotsk which had been tagged as far away as the southern part of the Japan Sea and on the outer (Pacific Ocean) side of the Kurils. The results of these and other Asian experiments in the years 1917 to 1942 are summarized by Hirano (1953). During about the same period many tagging experiments on Pacific salmon were performed in coastal areas of North America. Coastal tagging operations, not forming part of the INPFC program, have also been carried out more recently both on the western and eastern sides of the North Pacific. These are referred to in the present account only in cases where the findings contribute to an understanding of the distribution and movements of pink salmon in offshore or distant waters.

Tagging was first applied to the problem of determining the continental origin of salmon in mid-ocean areas by United States investigators, who conducted extensive operations in the Aleutian area in 1956. Widespread tagging experiments in high seas areas have been carried out since then by United States, Japanese and Canadian agencies. A summary of these operations, insofar as they involved pink salmon, is shown in Table 2, which indicates the distribution of tagging effort between various broad regions of the total high seas territory known to be occupied by pink salmon. These regions, formed by arbitrarily grouping stations occupied during the tagging expeditions, are shown in Figure 5.

The problem of catching a sufficient number of salmon in sufficiently good condition for tagging and release, under the conditions commonly prevailing in high seas fishing, has been attacked principally by the use of two different kinds of gear. After previous experimental operations United States investigators in 1956 and subsequent years have relied on purse seines to provide the required fish. A detailed description of the gear and its operation is given by Hartt (1962). Japanese investigators tagged gillnet-caught fish in 1957 but recoveries were few and in subsequent years reliance was successfully placed on longlining. This gear consists of a light cotton mainline, which is floated at the surface, with monofilament nylon gangings, about a meter in length, spaced at intervals of about three meters. The hooks are usually baited with salted whole anchovies. With Japanese technical assistance this gear was also used successfully by Canadian vessels for high seas tagging operations in the Gulf of Alaska in 1961 and 1962.

Both " disc " and " tube " tags were used in the United States experiments of 1956 to 1958 inclusive. They are described by Hartt (1962). Since then discs have been used exclusively by United States investi-

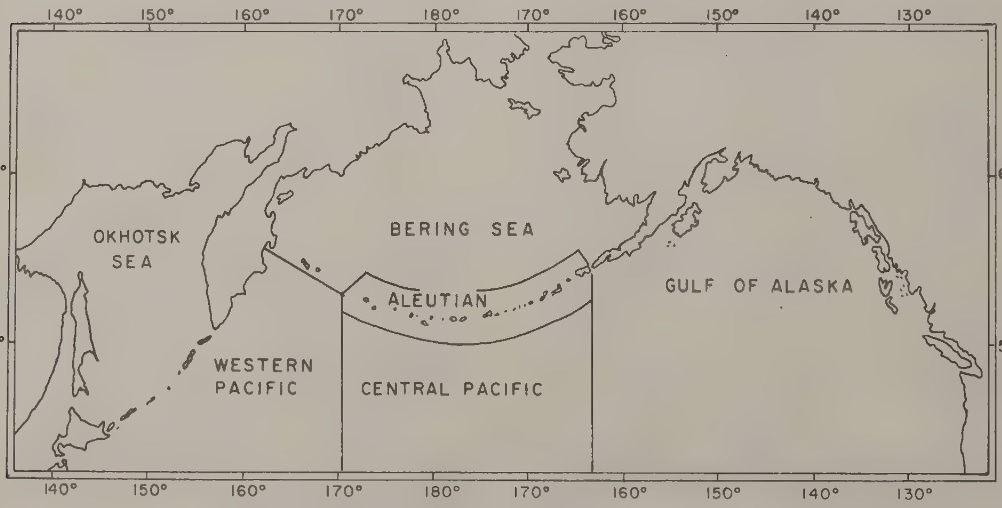

Figure 5. Tagging regions of North Pacific and adjacent waters.

gators and also in all Canadian operations. Japanese taggers used " Atkins " tags (a celluloid plate attached by copper wire) and a small number of tube tags in 1957 ; tubes in 1958 and 1959 ; discs and tubes in 1960 ; discs in subsequent years. Characteristics of the tags and methods of affixing them are described in INPFC (1958, 1959, 1961).

Because of the above-noted differences in fishing methods and kinds of tags, as well as the previously mentioned uncertainties concerning fishing intensity, recovery effort and the mortality associated with the varying time periods between tagging and recovery, it is not possible to make close comparisons between the quantitative results of the experiments listed in Table 2. It is evident, however, that recovery rates were relatively low in all instances. Recoveries of pink salmon from all the INPFC taggings conducted up to the end of 1961 amounted to about 3.5 percent. Total inshore and freshwater recoveries were not more than 2.0 percent. These figures are considerably lower than those reported for sockeye in the same experiments. In 1962, however, the pink salmon taggings carried out in the Gulf of Alaska yielded 8.0 percent recoveries.

It is noteworthy that except for the taggings in the Gulf of Alaska about two-thirds of all the pink salmon tagged in high seas operations were caught in June and less than 10 percent were caught earlier in the season. While the distribution of the various stocks during the summer fishing season of course has special significance, it is clear that by the time when most of the tagging was done a great many fish had already made extensive migrations from areas occupied earlier in the year. It is also obvious that even in the summer period it has not been possible with available resources to provide comparable coverage for all parts of the vast ocean regions inhabited by salmon.

Information derived from tagging experiments on the ocean distribution of pink salmon associated with major coastal regions of Asia and North America is presented in the following paragraphs. In Figures 6 to 13 the association between high seas localities and coastal regions is based entirely on recoveries made close inshore or in fresh water. In the case of pink salmon tagged in the Aleutian region, the evidence provided by coastal recoveries regarding the ocean distribution of a stock is strongly supported by recoveries made at intermediate localities on the high seas. Such high seas recaptures are shown separately in Figures 14 to 17. On the other hand, experiments conducted in the western Pacific have sometimes produced numerous high seas recoveries in many directions and at insufficient distances from the tagging points to provide good clues as to destinations. High seas recoveries of this type are not dealt with in detail in this report.

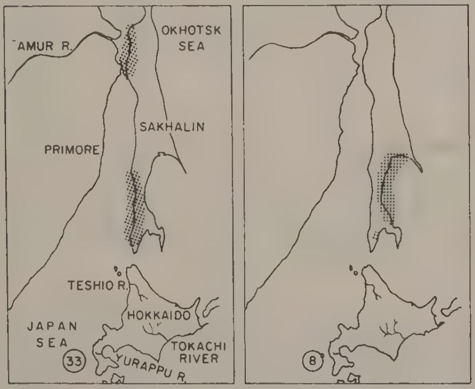

FIGURE 6. Tagging localities of pink salmon recovered from Sakhalin Island (April 24-May 17, 1958–1960). Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded areas.

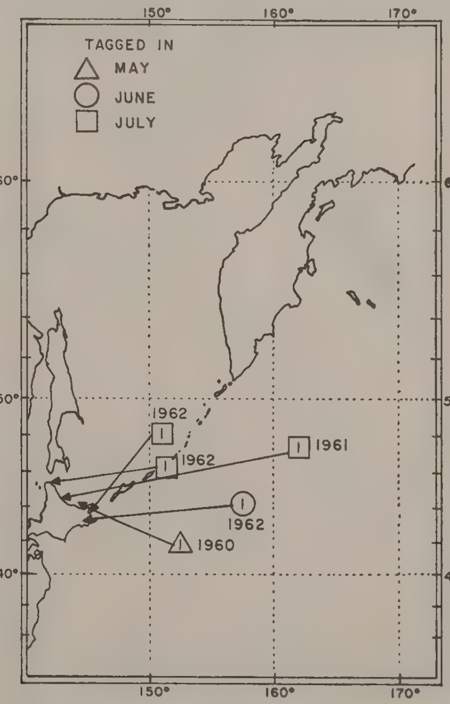

FIGURE 7. Tagging localities of pink salmon recovered from Hokkaido. Symbol shows tagging locality. Enclosed numeral shows number of recoveries.

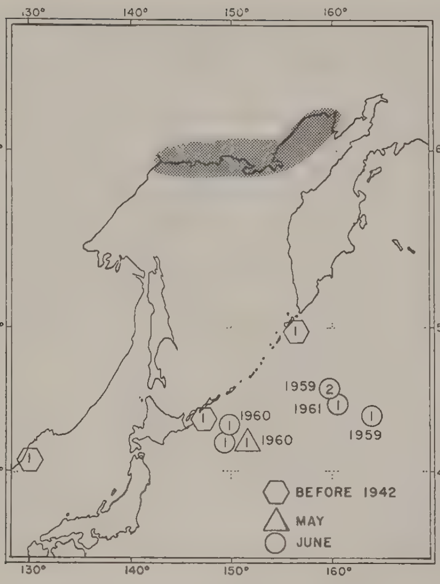
130°
140°
150°
160°
60°
50°
40°
1959
1961
1960
1960
1959
BEFORE 1942
MAY
JUNE

FIGURE 8. Tagging localities of pink salmon recovered from the north coast of the Okhotsk Sea. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

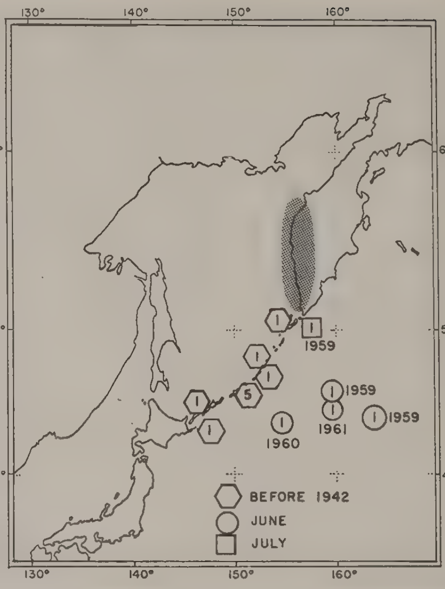
130°
140°
150°
160°
60°
50°
40°
1959
1959
1961
1959
1960
BEFORE 1942
JUNE
JULY

FIGURE 9. Tagging localities of pink salmon recovered from West Kamchatka. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

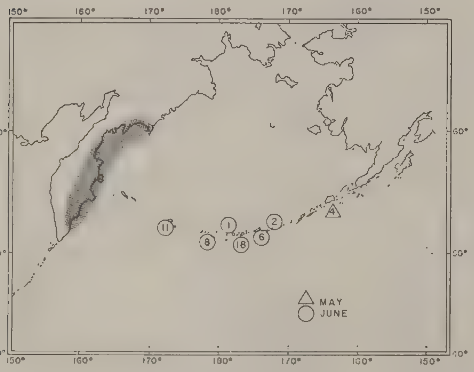
150°
160°
170°
180°
170°
160°
150°
60°
50°
40°
MAY
JUNE

FIGURE 10. Tagging localities of pink salmon recovered from East Kamchatka region, 1957. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

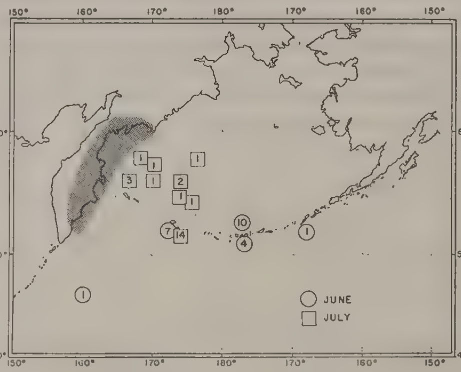
150°
160°
170°
180°
170°
160°
150°
60°
50°
40°
JUNE
JULY

FIGURE 11. Tagging localities of pink salmon recovered from East Kamchatka region, 1959. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

References to sources of information on high seas tagging and recoveries are given in Table 2. In cases where additional information was provided by coastal taggings, a reference is given in the text.

Results by regions

Primore. No pink salmon tagged outside the confines of the Japan Sea have yet been reported from streams or inshore localities of this region. Within the Sea, Hirano (1953) records recoveries in 1928–29 of fish tagged as far south as the Korean coast at about Latitude 40°N. Others, tagged off the southern end of Hokkaido in April and May, 1958, 1959 and 1960, have been noted by Ishida (1961).

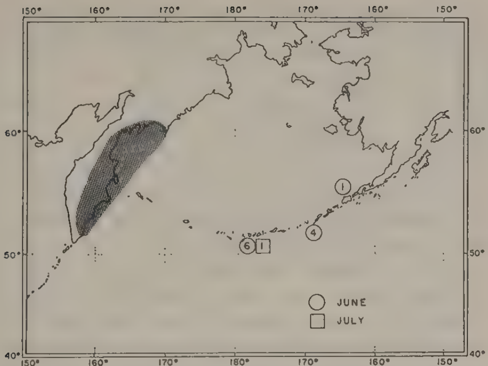
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
1
4
6
1
JUNE
JULY

FIGURE 12. Tagging localities of pink salmon recovered from East Kamchatka region, 1961. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

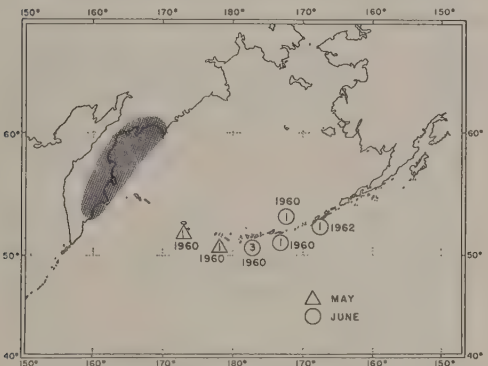
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
1960
1
1962
1
1960
1
1960
1960
3
1960
MAY
JUNE

FIGURE 13. Tagging localities of pink salmon recovered from East Kamchatka region, 1960 and 1962. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

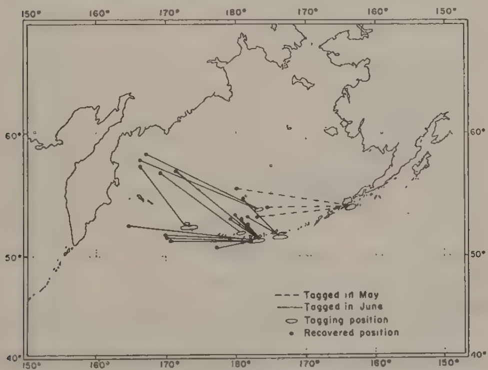
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
Tagged in May
Tagged in June
Tagging position
Recovered position

FIGURE 14. Tagging and recovery localities of pink salmon tagged in the Aleutian region and recovered on the high seas, 1957.

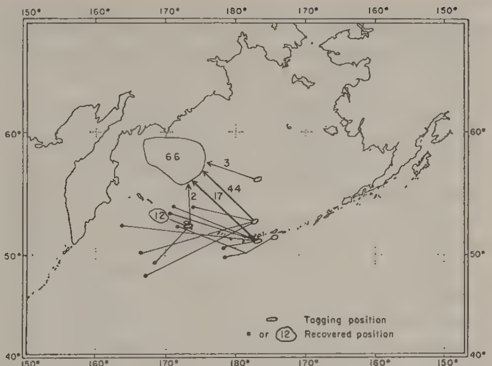
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
66
3
44
17
2
12
Tagging position
or 12 Recovered position

FIGURE 15. Tagging and recovery localities of pink salmon tagged in the Aleutian and Bering Sea regions in June 1959 and recovered on the high seas.

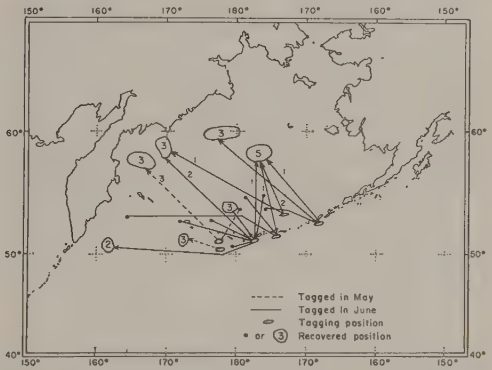
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
3
3
3
5
2
1
3
3
3
2
Tagged in May
Tagged in June
Tagging position
or 3 Recovered position

FIGURE 16. Tagging and recovery localities of pink salmon tagged in the Aleutian region in 1960 and recovered on the high seas.

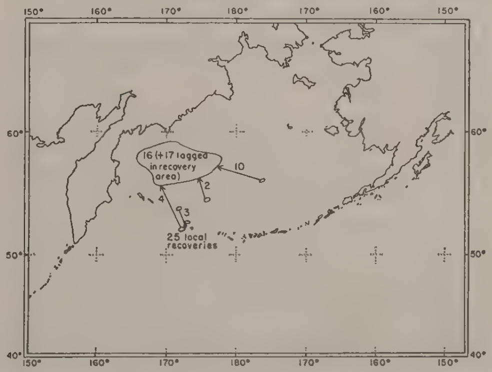
150° 160° 170° 180° 170° 160° 150°
60°
50°
40°
16 (+17 tagged in recovery area)
10
2
4
3
25 local recoveries

FIGURE 17. Tagging and recovery localities of pink salmon tagged in the Aleutian and Bering Sea regions in July 1959 and recovered on the high seas.

Amur River district. Information on the ocean distribution of Amur pink salmon is the same as for Primore, except that no recoveries were reported from the 1959 taggings off southern Hokkaido.

Sakhalin Island (Fig. 6). Recoveries on both the west and east coast of Sakhalin Island were forthcoming from the Japan Sea taggings off southern Hokkaido in April and May, 1958, 1959 and 1960. East coast recoveries have been made also from relatively southern areas of the North Pacific Ocean, namely near the eastern coasts of Hokkaido and the southern Kurils (Hirano, 1953), from 46°N, 160°E (June 1959) and from near 42°N, 150°E (June 1961).

Hokkaido (Fig. 7). A few tagged pink salmon were recovered from inshore and freshwater localities in Hokkaido in 1960, 1961 and 1962. The easternmost tagging locality for these fish was at 47°N, 162°E in July 1961.

Northern coast of Okhotsk Sea (Fig. 8). A long journey by a pink salmon from the Korean coast to the Okhotsk district is reported by Hirano (1953), who also mentions migrants to this region from the Pacific Ocean side of the Kurils in pre-war years. Recent odd-year taggings show an eastward range as far as 46°N, 160°E and 44°N, 164°E in June 1959, and 45°N, 160°E in June 1961. In 1960 fish were recovered from taggings at 42°N, 151°E (May), 42°N, 149°E (June), and 43°N, 150°E (June). A close approach to this coast was shown by a fish tagged in May 1962 at 42°N, 154°E.

West coast of Kamchatka (Fig. 9). The pre-war taggings showed pink salmon migrating to this region from the northern and southern Kurils (Hirano, 1953). Recent high seas taggings by Japanese investigators have yielded the following single returns: 1959: 44°N, 164°E (June), 46°N, 160°E (June), 50°N, 158°E (July); 1960: 44°N, 155°E (June); 1961: 45°N, 160°E (June).

Okhotsk Sea stocks in general. The known Pacific Ocean distribution of all Okhotsk Sea stocks of pink salmon (Hokkaido, Sakhalin I., North Coast and West Kamchatka) is relatively southerly and is quite limited in an eastward direction. None of the coastal recoveries have come from taggings made farther east than 164°E. In 1958 Japanese taggings in the western Pacific (July) resulted in 10 high seas captures within the Okhotsk Sea. While the ultimate destinations of these fish are not known, none of them had been tagged farther east than 165°E. There is, however, a possibility that pinks from the Okhotsk Sea and/or the Sea of Japan may range farther east at seasons other than those at which extensive taggings have been made.

East Kamchatka, Karaginskii and Oliutorskii regions (Figs. 10–17). Taggings in 1957 showed that pinks from this region were present in May at the eastern end of the Aleutians (54°N, 164°W). In June they were found along the Aleutian chain from 173°E to 172°W. A total of 50 tag recoveries was made in Asian coastal waters and 19 additional tags were recovered at high seas localities in the same direction.

In 1958 no tags were recovered in this region and pink salmon were scarce at the Aleutian localities where tagging was carried out.

In 1959 recoveries were made from fish tagged in June along the Aleutian chain from 172°E to 168°W (a total of 22 coastal recoveries) and one from 46°N, 160°E. Twenty-five fish tagged in July at the western end of the Aleutians and in the western part of the Bering Sea were also recovered at inshore localities. In addition, numerous fish were recovered at high seas localities between the tagging points and the Karaginskii coast.

Recoveries of fish tagged in 1960 included single individuals tagged in May at 173°E and 177°E in the Aleutian area, and five fish tagged in June at 177°W and 174°W. Other pinks tagged in June at these localities and as far east as 168°W had moved in the same general direction when recaptured on the high seas.

June taggings in 1961 at Aleutian localities from 177°W to 165°W again yielded coastal recoveries (12) from the Karaginskii district and one fish tagged at 177°W in July was recaptured at an uncertain locality on the Asian coast.

In 1962, a pink salmon tagged in June at 53°02′N, 167°42′W was recovered in Karaginskii waters.

Although data obtained after 1962 have been excluded from the tables and figures of the present report, it is desirable to mention that taggings made in 1963 showed an eastward extension of the ocean range occupied by Asian pink salmon beyond that which was demonstrated by previous taggings. In 1963, recoveries were made not far from the Karaginskii coast of five fish tagged by a United States vessel in June at localities between 162°W and 158°W (latitude 48°N–52°N) and four others tagged by a Canadian vessel in May at localities from 160°W to 155°W in the same region (latitude 47°N–51°N). Three additional recoveries provided evidence of the presence of Asian fish in inshore Alaskan waters at 54°41′N, 163°10′W in June. These various 1963 recoveries are reported in INPFC (1964b).

Northwestern coast of Bering Sea. This appears to be a relatively unimportant area for pink salmon. Single recoveries have been reported from an Aleutian tagging near Adak (June 1959) and at 54°N, 174°W (June 1960). In the latter year four fish tagged in

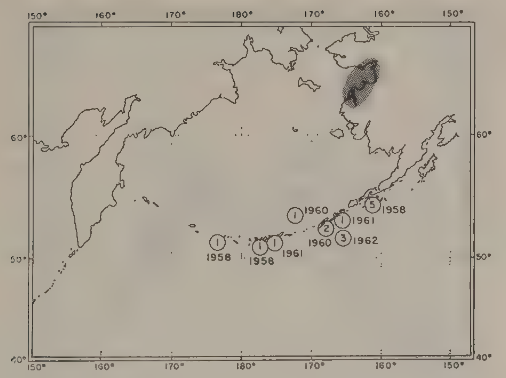

FIGURE 18. Tagging localities of pink salmon recovered from Norton Sound and Yukon River. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

June at 168°W were recovered at high seas positions in the direction of this coastline.

Norton Sound and Yukon River (Fig. 18). From taggings at Aleutian localities between 177°E and 167°W in June of 1958, 1960 and 1961 a few pink salmon were recovered in this area. In 1958 taggings made by the U. S. Bureau of Commercial Fisheries on the south side of the Alaska Peninsula in June and early July yielded five returns from Norton Sound and the Yukon River (Thorsteinson, 1959). In 1962, three fish tagged in June near 53°N, 168°W were recovered in Norton Sound. An additional fish, tagged far to the southeast (47°N, 137°W) in April was recovered from fresh water on St. Lawrence Island, a journey of about 2,700 kilometers.

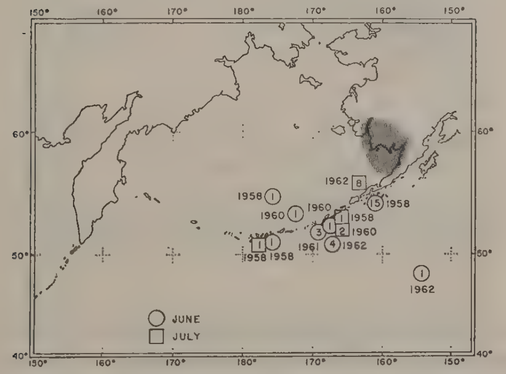

FIGURE 19. Tagging localities of pink salmon recovered from Bristol Bay area. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

Kuskokwim and Bristol Bay (Fig. 19). No recoveries were reported from this area in 1957 and 1959. In 1958 fish were present near Adak (177°W) in June and July; at 55°N, 176°W (Bering Sea) in June; at 53°N, 167°W in July. Fifteen recoveries were made from June and early July taggings on the south side of the Alaska Peninsula (Thorsteinson, 1959).

In 1960 a fish tagged in June at 53°N, 173°W, and two tagged in July at 53°N, 167°W were recovered in Bristol Bay.

In 1961, June taggings at 53°N, 169°W yielded three returns.

In 1962, four pinks tagged in June on the south side of the Aleutians, near 167°W, were recovered from Bristol Bay. Another Bristol Bay recovery came from considerably farther to the southeast (48°N, 154°W). Eight additional recoveries were of fish tagged in the eastern Bering Sea, near 56°N, 165°W.

Gulf of Alaska. No significant numbers of pink salmon were tagged on the high seas of the Gulf of Alaska prior to 1961. In that year about 2,000 maturing fish were released, mainly in northeastern, northern and northwestern areas of the Gulf. In 1962 extensive coverage of waters between Latitude 45°N and Latitude 58°N was provided by Canadian and United States tagging vessels. The release of 10,000 tagged pinks yielded 846 recoveries.

For present purposes three main coastal regions of pink salmon abundance within the Gulf are recognized. The distribution of the tagged fish which proceeded to these regions is shown in Figures 20 to 25., Because of the large numbers of tags and positions involved, these are grouped by areas representing two degrees of latititude and five degrees of longitude.

Taggings conducted in 1961 showed that pink salmon from the *northwestern Gulf of Alaska* (Figs. 20 and 21) occurred within a large region in the north and west-central part of the Gulf in July, but did not indicate the whereabouts of the fish in the earlier part of the season, nor the total area occupied in any month.

Recoveries of fish tagged in April and May 1962 showed that at this season the pink salmon of this coastal region were distributed at relatively distant localities to the south and east. In fact no pink salmon were caught before June within a large high seas area adjacent to the northern and western coastline of the Gulf. The total range of distribution exhibited during the course of the season extended from 130°W to 157°W and from 45°N to 59°N—thus practically covering the whole of the Gulf.

The 1961 tag recoveries in *southeastern Alaska* (Figs. 22 and 23) were mainly from fish caught in July in

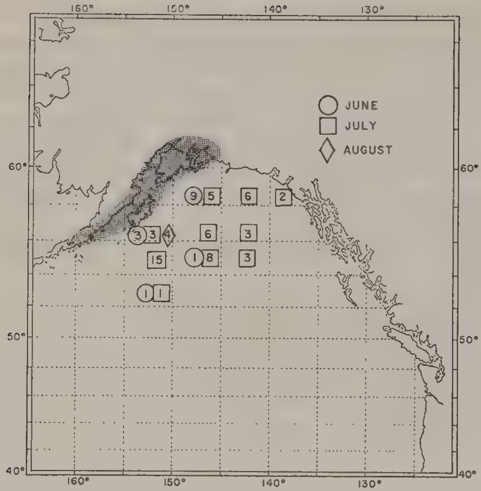
160°
150°
140°
130°
JUNE
JULY
AUGUST
60°
50°
40°
9
5
6
2
3
3
6
3
15
1
8
3
1
1

Figure 20. Tagging localities of pink salmon recovered in northwestern coastal area of Gulf of Alaska, 1961. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

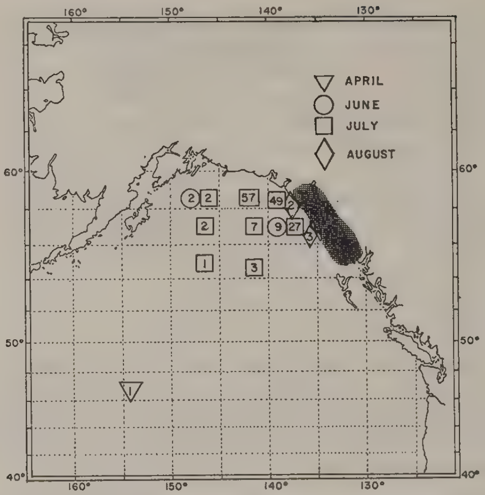
160°
150°
140°
130°
APRIL
JUNE
JULY
AUGUST
60°
50°
40°
2
2
57
49
2
2
7
9
27
3
1
3
1

Figure 22. Tagging localities of pink salmon recovered in southeastern Alaska, 1961. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

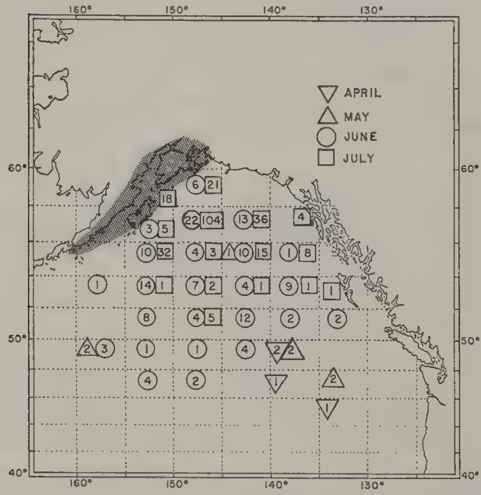
160°
150°
140°
130°
APRIL
MAY
JUNE
JULY
60°
50°
40°
6
21
18
22
104
13
36
4
3
5
10
32
4
3
1
10
15
1
8
1
14
1
7
2
4
1
9
1
1
8
4
5
12
2
2
2
3
1
1
4
2
2
4
2
1
2
1

Figure 21. Tagging localities of pink salmon recovered in northwestern coastal area of Gulf of Alaska, 1962. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

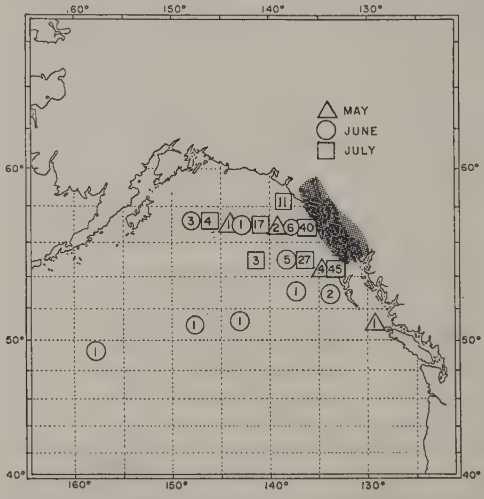
160°
150°
140°
130°
MAY
JUNE
JULY
60°
50°
40°
11
3
4
1
1
17
2
6
40
3
5
27
4
45
1
2
1
1
1
1

Figure 23. Tagging localities of pink salmon recovered in southeastern Alaska, 1962. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

the northern and northeastern part of the Gulf. There was, however, one recovery of an early-season fish tagged far to the southwest by a Japanese vessel.

The better coverage in space and time which was effected in 1962 yielded recoveries of fish tagged in May, June and July in the northern and eastern part of the Gulf. The pattern of distribution was in general much more restricted than that shown by recoveries for the northwest region of the Gulf although single individuals came from June taggings extending southwestward to as far as 49°N, 157°W—near the location of the Japanese tagged fish recovered in 1961.

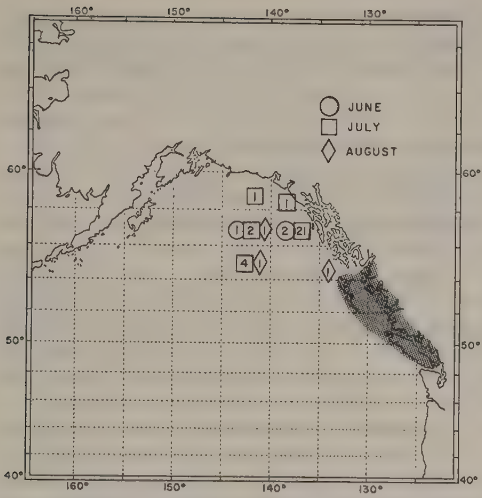

FIGURE 24. Tagging localities of pink salmon recovered in British Columbia, 1961. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

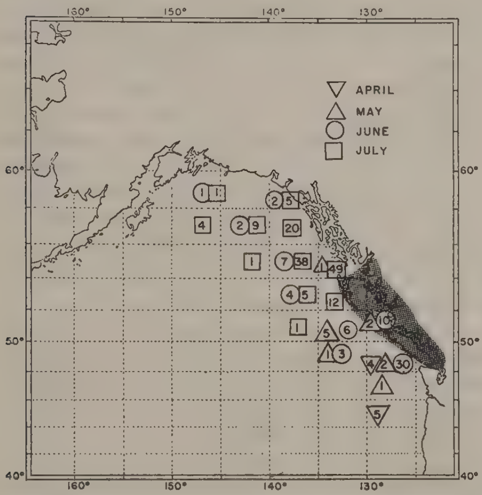

FIGURE 25. Tagging localities of pink salmon recovered in British Columbia, 1962. Symbol shows tagging locality. Enclosed numeral shows number of recoveries made in shaded area.

Recoveries in *British Columbia* (Figs. 24 and 25) showed that in April 1962 pink salmon of this area occurred as far south as 45°31′N off the Oregon coast. A northward movement during the progress of the season was evident and many fish tagged in July were far to the north of their recovery areas. The northern part of the total range shown by British Columbia pink salmon coincided closely with that of southeastern Alaskan fish. Westward range, during the period of the tagging operations, appeared to be decidedly restricted.

It may be pointed out that the good coverage of the Gulf which was effected in 1962 naturally failed to disclose the high seas distribution of the large pink salmon populations which migrate to southern British Columbia and Washington in " odd " years.

Summary

From the tagging experiments conducted up to the end of 1962 :

(1) There is as yet no evidence that stocks breeding in Primore and in the Amur River basin occur outside the confines of the Sea of Japan, although it certainly cannot be affirmed that such fish are not present at times in parts of the Sea of Okhotsk.[1]

(2) Fish breeding in the watersheds of the Sea of Okhotsk have not been identified from farther east than 165°E in an odd year (1959) and 155°E in an even year (1960).

(3) East Kamchatkan stocks were present in numbers along the Aleutian chain in the odd years 1957, 1959, 1961. The easternmost localities for recovered fish were at about 164°W (1957 and 1961) and 155°W (1963). In the even year 1958 no recoveries were reported from Aleutian taggings. In 1960 and 1962 the presence of East Kamchatkan fish in the Aleutian region to as far east as 168°W was indicated.

(4) Norton Sound pink salmon have been tagged (in June) at localities near the Aleutian Islands to as far west as 177°E in an even year (1958) and 176°W in an odd year (1961). The recovery at St. Lawrence Island of a fish tagged in April 1962 less than 500 miles off the Washington coast suggests that some pink salmon from the northern Bering Sea may penetrate far into the Gulf of Alaska in the earlier months of the year.

(5) Pink salmon stocks breeding in the northern and western coastal areas of the Gulf of Alaska are found mainly in eastern and southern parts of the Gulf in April and May, to as far south as 45°N. They move north and northwest with the progress of the season.

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[1] Identification of hooks found in pink salmon in the Amur Estuary as being of Kuril origin is mentioned by Ricker (1962, p. 198, footnote). Taggings in the Kuril region have yielded recoveries of chums, but not pinks, from the Amur. Birman (1964) mentions the capture of pink salmon carrying longline hooks along the *western coast of Kamchatka* (this would conform with the tagging data) but does not seem to make such a statement for the Amur.

(6) Stocks breeding in southeastern Alaska have not been extensively reported from the western part of the Gulf region although isolated recoveries of fish tagged in April and June near 155°W suggest that early season distribution may be wider than has hitherto been demonstrated. Canadian fish have not been reported from the central and western parts of the Gulf except in the extreme north.

(7) There is no evidence from tagging experiments that pink salmon originating in the Gulf of Alaska ever leave that general region. There is much evidence, however, that fish originating in Bering Sea areas are present in the Gulf in spring and early summer.

(8) The information provided by tagging experiments on the high seas distribution of most of the coastal stocks recognized in this report is in large measure confined to a seasonal period extending only from May to July. Except for recent operations in the Gulf of Alaska in April, the distribution of stocks at earlier stages of their ocean life remains virtually unknown.[2]

Evidence from Scales, Meristic and Non-Meristic Characters

United States and Japanese research workers have attempted to determine the regions of origin of pink salmon caught on the high seas by means of scales or meristic characters (Pacific Salmon Investigations, 1958a, b, c ; Ishida and Miyaguchi, 1958, 1959a, b ; Amos *et al.*, 1963 ; Ishida, 1960, 1961 ; INPFC, 1963 ; Miyaguchi and Kyushin, 1961). Although the findings of these studies vary somewhat in the accuracy attained in the separation of stocks, depending on the method used and amount of data available, the main conclusions are essentially the same. Observations of meristic characters and scale patterns revealed as early as 1958 that Asian pink salmon could be fairly well separated from pinks originating in the southern parts of the North American coast, particularly in southeastern Alaska and southward, although they could not readily be distinguished from pinks originating in the Aleutian Islands, the Alaskan coast of the Bering Sea and the southern side of the Alaska Peninsula. Since then, United States investigators have placed emphasis on the problem of distinguishing East Kamchatkan pinks from western-central Alaskan pinks, since intermingling of these stocks was known to take place on the high seas, and have attempted to estimate the proportions of high seas caught pinks originating in the two continents by discriminant function analysis. They have also searched for new characters that would give better separation than those used previously. Japanese investigators have continued to study scales but have made no observations on meristic characters.

Scale characters used and their effectiveness

Certain attempts to distinguish pink salmon originating in different geographical regions by scales were made before the commencement of the INPFC research program. The Hokkaido Prefectural Fisheries Experimental Station (1956) and Yamashiro (1958) classified pink salmon from Hokkaido streams, the Japan Sea, Pacific waters off the Kuril Islands and Aleutian waters into several types by using the pattern of the center portion, intervals between circuli, number of circuli constituting the resting zone, etc., and studied the proportions of pinks with different types of scale pattern in different geographical regions. Hayashi (1957) studied the scales of 116 pink salmon collected by the research vessel *Tenyo-maru* in the northwest Pacific during 1952–54. He suggested that such characters as the circulus count, position of the resting zone, calculated length at the time of formation of the resting zone, etc., may be useful for distinguishing stocks, because they showed rather small variations within the same areas in the same years, although their variations in different years were considerable. Miyaguchi and Ishida (1957) studied pink salmon scale samples, collected from Hokkaido streams, the Japan Sea and the northwest Pacific during 1952–56, in an attempt to express the differences in scale pattern in terms of certain measurements, and suggested that some of these measurements might be useful for distinguishing pink salmon stocks.

A common problem in studying scales to determine racial origin is the error caused by scales collected from different portions of the fish body. Scales collected under the INPFC program from 1957 on have been taken from an assigned body area, i.e., from three or four rows above or below the lateral line and within the anterior half of the range from the posterior end of dorsal fin to adipose fin. If a sample is taken from some other area, it should be recorded. According to Pacific Salmon Investigations (1958b, 1958c), scale samples in 1955 and 1956 were taken from the same assigned area whenever it was possible, but were taken from the nearest available area when there were no scales in the assigned area, without keeping record. However, scales sampled in 1955 and 1956 are not different from those taken in 1957 and later in the incidence of regenerated, absorbed or abnormal scales. Ishida and Miyaguchi (1959b) omitted scales that were apparently taken from other areas (judging from shape), and also took into consideration biases in the two characters measured which might have been caused by differences in the scale sampling area.

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[2] In August-October 1964, approximately 1,015 juvenile pink salmon were tagged in the northeastern Gulf of Alaska by a United States research vessel. Recoveries from this operation are not yet forthcoming.

The scale characteristics used for the purpose of distinguishing pink salmon stocks under the research program of the INPFC are listed in Tables 3 and 4. There are 14 such characters. Many of these characters are either related to each other or similar to each other. There are such similarities or relationships within each of the following groups: characters 1–3, 4–7, 8–11, and 12–14. In the following paragraphs the more widely used characters are discussed briefly.

Table 3. Scale characters used in the racial studies of pink salmon.

	Character definition
1.	Number of circuli from the focus to the annulus.
2.	Scale length from the focus or center ring to the annulus.
3.	Ratio of the number of circuli to the scale length of the yearly growth zone.
4.	Number of circuli in the first (and second) half of the distance from the outermost edge of the center ring to the annulus.
5.	Number of circuli in the first, second and last third of the distance from the outermost edge of the center ring to the annulus.
6.	Number of circuli in the first, second, third, fourth, fifth and last sixth of the distance from the outermost edge of the center ring to the annulus.
7.	Ratio of the number of circuli in the first half of the distance from the outermost edge of the center ring to the second half number.
8.	Scale length to the tenth circulus from the focus or center ring.
9.	Scale length from the center ring to the sixth circulus.
10.	Scale length between the fourth and tenth circulus.
11.	Length of narrowest band of three successive circuli interspaces included between circuli 1–10 (either circuli 1 to 4, 4 to 7, or 7 to 10).
12.	Length of scale four interspaces outside (beyond) the annulus.
13.	Length of scale four interspaces inside the annulus.
14.	Number of circuli in the distance of 0.5 mm outside the annulus.

Number of circuli from the focus to the annulus. This character has been used by all scale workers. The circulus counts used by different workers are only slightly different from each other. They are the number of circuli from the focus of the scale to the annulus (Amos *et al.*, 1963), number of circuli from the focus to the outer edge of the annulus (Mosher *et al.*, 1961) or the number of circuli from the focus to (and inclusive of) the first circulus of the new spring growth zone (Ishida and Miyaguchi, 1959b). Slightly different counts are obtained depending on the radius chosen. There were no significant differences in the repeated readings by the same readers or between the readings of different readers (Pacific Salmon Investigations, 1958b). Ishida (1961) and Miyaguchi and Kyushin (1961) studied separately the same scale samples, but there were no significant differences between the counts obtained.

Intra-area variations by sex and size were examined. Amos *et al.* (1963) reported that 4.26 percent of the intra-area variation was accounted for by differences in size, but that there were no differences between sexes. Ishida and Miyaguchi (1959b) pointed out that among pink salmon caught in the same high seas areas males tended to show larger counts than females and fish in early samples tended to show larger values than those in late samples. However, these observations actually do not add anything to the conclusions obtained by Amos *et al.* Male pinks are larger in size than female pinks and larger pinks tend to be caught selectively during the first half of the fishing season of the Japanese high seas fishery because of gillnet selectivity.

Table 5 shows the mean circulus counts in the first-year zone for pinks from the coastal areas and

Table 4. Scale characters used in racial studies of pink salmon.

Author	Scale Character													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*
Pacific Salmon Investigations (1958 b)	×	×	×					×						
Ishida and Miyaguchi (1958)	×													×
Ishida and Miyaguchi (1959 a)	×													×
Ishida and Miyaguchi (1959 b)	×													×
Mosher *et al.* (1961)	×	×		×				×	×	×	×	×	×	
Ishida (1960)	×													
Pearson (1963)	×			×		×					×			
Miyaguchi and Kyushin (1961)	×		×				×							
Ishida (1961)	×													
Amos *et al.* (1963)	×	×						×						

Table 5. Average number of circuli in the first-year growth of pink salmon sampled from North American and Asian coastal areas and high seas in 1955–1960 (Ishida, 1961).

Area	1955		1956		1957		1958		1959		1960	
	M	F	M	F	M	F	M	F	M	F	M	F
Coastal samples												
Abashiri, Hokkaido							23.7		24.3			
Datta Bay, Primore											20.4	20.0
Amur River											19.6	19.6
Sakhalin											21.5	21.4
Okhotsk coast											19.7	20.1
Taui River											19.7	19.7
Icha River											19.4	19.7
Bolshaia River											20.3	19.7
Unalakleet			20.9	20.7			23.0	23.4	24.1			
Nushagak							24.5	24.9				
Alaska Peninsula	21.8	21.4	19.6	19.4	22.2	21.5	23.4	23.5	23.8			
Kodiak Island			20.5	21.4	22.2	22.0	25.9	25.2	24.0			
Cook Inlet	24.1	23.3	18.6	18.2	21.4	21.6	23.1	22.8				
Prince William Sound					24.8		28.5	29.2	28.4			
Yakutat							28.9	28.0				
Petersburg	27.4	26.9	23.1	21.5	23.6	23.2	27.0	27.2	27.4			
Ketchikan	28.3	28.1	25.9	23.7	26.6		28.7	29.3	30.0			
Nass River	28.5	28.5	24.4	24.9	25.8	26.1	28.0	28.0				
Skeena River	27.6	26.9	24.5	25.4	25.8	25.5	27.9	27.6	29.1	28.8		
Bella Coola									30.5	30.3		
Rivers Inlet			26.1	25.3			29.8	30.5	32.0	30.9		
Smith Inlet									30.1	30.0		
Fraser River	28.2	27.8			29.1	28.5			29.9			
High seas samples												
Japan Sea (off Hokkaido) landbased fishing grounds	22.2	22.5	22.7	22.5	20.0	20.1	20.2	20.4	20.7	21.7	20.2	19.9
May									21.1	21.3	20.1	19.5
June							21.5	20.9	21.7	21.7	20.5	20.6
July							21.4	21.5	21.5	20.7	20.3	20.7
August							22.8	22.1	22.9	22.5		
Mothership fishing grounds												
N. W. Pacific, May–E. June			22.9	22.6	21.2	20.8	22.7		21.4	21.3	21.1	
N. W. Pacific, M.–L. June							22.4	22.1	21.4	20.7	20.8	
N. W. Pacific, July							22.2	22.2	20.0	19.9	21.8	
Bering Sea, May–E. June					21.2	21.4	22.5	22.1				
Bering Sea, M.–L. June							22.2	22.2			21.6	21.1
Bering Sea, July							22.6	22.3	21.3	21.4	21.7	21.7

streams of Asia and North America and from the high seas during 1955–60 as given by Ishida and Miyaguchi (1959a) and Ishida (1961). Geographical position of coastal localities mentioned in Table 5 and elsewhere in this section are shown in Figure 26.

In general, the mean count for North American pinks decreases from the south to the north. It drops sharply between Prince William Sound and Cook Inlet, the value for Cook Inlet being the lowest. Values for the Alaska Peninsula and the Bering Sea coast of Alaska are slightly higher than those for Cook Inlet. The mean circulus counts for pink salmon in the various areas of the Gulf of Alaska coast have shown considerable year-to-year variations, which have tended to be parallel in different areas. The counts were lowest in 1956 and gradually increased thereafter to 1959. These general trends appeared to be in conformity with the trends of variation in weight of British Columbia pinks as recorded by Godfrey (1959).

The mean counts for western and central Alaskan pinks tend to be slightly larger than those for pinks caught by the mothership fishery in the western Bering Sea. Although the amount of difference has also changed from year to year, being less than 1.0 in 1957 and over 2.0 in 1959, from tagging results

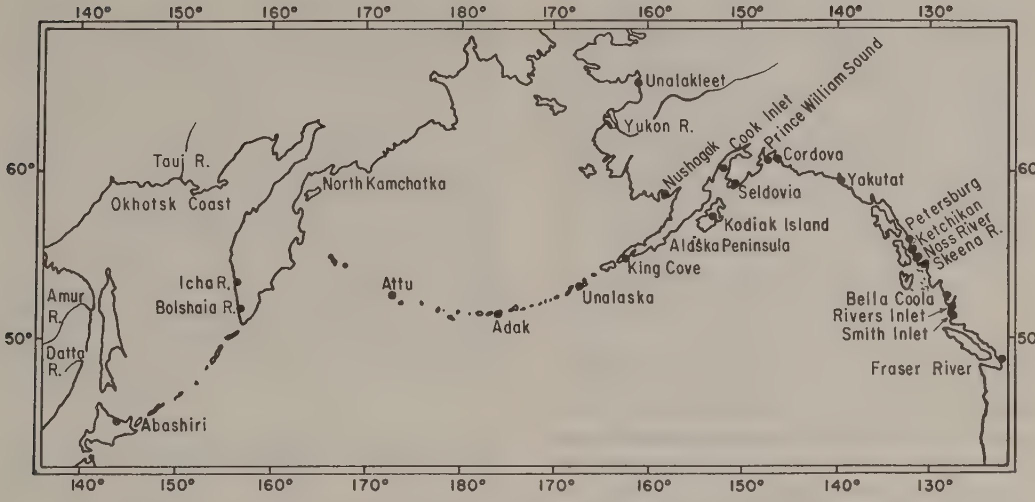

140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
Unalakleet
Yukon R.
Nushagak
Cook Inlet
Prince William Sound
Cordova
Yakutat
Seldovia
Kodiak Island
Alaska Peninsula
King Cove
Unalaska
Petersburg
Ketchikan
Nass River
Skeena R.
Bella Coola
Rivers Inlet
Smith Inlet
Fraser River
Adak
Attu
North Kamchatka
Tauj R.
Okhotsk Coast
Icha R.
Bolshaia R.
Amur R.
Datta R.
Abashiri

FIGURE 26. Location of North American and Asian coastal sampling areas for years 1955–1960.

it appears that the overwhelming majority of the pink salmon caught by the mothership fishery in the Bering Sea in these years were East Kamchatkan fish.

The mean counts for pink salmon from various high seas and coastal areas on the Asian side (including East Kamchatkan pinks) are more or less similar to each other, except for pinks from Hokkaido streams, and their year-to-year variations are also small. Hokkaido pinks show somewhat larger values than pinks from other areas of Asia.

The effectiveness of a character for distinguishing pink salmon originating in the two continents depends on the amount of difference in the same character between East Kamchatkan pinks and western-central Alaskan pinks. Amos *et al.* (1963) did not use the mean circulus counts in the first-year zone in the estimation (by discriminant function analysis) of the proportions of Asian and North American pinks in the high seas samples collected in 1957 because they found no significant difference between the Karaginskii samples and the Kodiak-Cook Inlet samples, which were chosen as morphotypes. However, the difference was great in 1959, increasing the usability of this character (Ishida, 1961). It is therefore desirable to examine the mean counts for these pinks every year in order to take advantage of large differences that might occur in some years.

The observed large differences in this character between pinks originating in the southeastern part of the Gulf of Alaska and those originating in the northern part of the Gulf may be very useful for determining the high seas distribution of these two groups of pinks, although this has no direct relation to the problem of distinguishing pink salmon from the two continents (Ishida and Miyaguchi, 1959b).

Scale length from the focus or center ring to the annulus. Pacific Salmon Investigations (1958b) and Amos *et al.* (1963) used the distance from focus to annulus and Mosher *et al.* (1961) adopted the distance from first circulus to annulus.

The effectiveness of this character in distinguishing pink salmon from the two continents has not been fully studied. However, Amos *et al.* (1963) report that it was not effective in 1957.

Ratio of the number of circuli to the scale length in the first-year growth. This character was used by Pacific Salmon Investigations (1958b) in the distance function analysis of pink salmon samples collected from various areas during 1955–1957, and the usefulness of this character was discussed by Miyaguchi and Kyushin (1961).

Although it is evident that pink salmon scales from British Columbia and southeastern Alaska have considerably more narrowly spaced circuli than those from other areas, this character does not seem to show great differences between East Kamchatkan pinks and western-central Alaskan pinks (Miyaguchi and Kyushin, 1961).

Other characters (listed as 4–7 in Table 3) which are associated with the spacing of circuli in different portions of the first-year zone have received some study. The variation in circulus spacing is, in general, greater in the first half of the first-year zone than in the last half (Miyaguchi and Ishida, 1957). This seems to be caused by what is called the "fry zone" by Milovidova-Dubrovskaia (1937) and Miyaguchi (1959). A "fry zone" consisting of five to eight narrowly spaced circuli at the center of the scale is sometimes present. The proportion of pink salmon scales with a fry zone varies somewhat from area to area, being, for example, higher for Japan Sea pinks than for northwest Pacific pinks. However, the frequency of occurrence of this character is not specific for various populations and it varies from year to year within the same populations.

Scale length from the focus or center ring to the tenth circulus. Length measurements between various circuli have also been tried. The scale length from the center to the tenth circulus was used by Pacific Salmon Investigations (1958b) and Amos *et al.* (1963) for distinguishing Asian and North American stocks. Amos *et al.* found that this character was the only effective one among the three scale characters used for discriminant function analysis. The percent contribution of this character to the total separation was approximately 23 percent.

Length of the narrowest band of three successive circuli between the first and tenth circulus (the first to fourth circulus, or the fourth to seventh circulus, or the seventh to tenth circulus). Pearson (1963) used this character with three circuli characters and two meristic characters on the 1959 samples with some success in distinguishing between Asian and American stocks. Its greatest contribution, however, was in separating out the Unalakleet samples.

Other length measurements between various circuli have also been tried, as indicated in Table 3.

Meristic and non-meristic characters

The earliest observations of the inter-area differences of the morphological characteristics of pink salmon are those made by Pravdin (1929, 1932) for West Kamchatkan and Amur pinks. More recently, Eniutina (1954) compared pink salmon spawning in the Amgun, a tributary of the Amur, with those spawning in the Iski River, Okhotsk district, for morphological differences. She states that no significant differences were found between these two groups in vertebral count, number of gill rakers, number of dorsal fin rays, number of anal fin rays and three other meristic characters but significant differences were found in some non-meristic characters. There were no studies of the morphological differences between Asian and North American pink salmon before the INPFC research program.

Under the INPFC research program, United States investigators studied the effectiveness of various meristic characters in distinguishing stocks and attempted to separate pinks originating in the two continents by using such characters (Amos *et al.*, 1963; Pacific Salmon Investigations, 1958c; Pearson, 1963).

Twenty morphological characters were examined in pink salmon samples collected from the Asian and North American coasts as well as from the high seas during 1955–57 (Pacific Salmon Investigations, 1958c). Six of these characters (the position of first complete haemal arch, number of caudal vertebrae, number of gill rakers on the ventral arm of the first left gill arch, number of branchiostegals on the left side of the head, number of fin rays in the left pectoral fin, and number of dorsal fin rays) were used for distinguishing stocks. According to Amos *et al.* (1963) only two (the number of vertebrae and number of dorsal fin rays) of the seven characters shown in Table 6 were useful for morphological separation of Asian (Karaginskii) pinks and North American (Kodiak-Cook Inlet) pinks sampled in 1957. The single scale character mentioned previously was added to these meristic characters, and the three characters were used for distinguishing Asian and North American pinks. The number of vertebrae contributed 62 percent of the total separation and the number of dorsal fin rays only four percent.

TABLE 6. Meristic characters examined for possible use in separating various populations of pink salmon.

Character	Author		
	Pacific Salmon Investigations (1958c)	Amos *et al.* (1963)	Pearson (1963)
Number of vertebrae		×	×
Position of first complete haemal arch	×		
Number of caudal vertebrae	×		
Number of gill rakers on ventral arm of first left gill arch	×	×	
Number of gill rakers on the first left gill arch		×	
Number of branchiostegal rays on left side of head	×	×	×
Number of left pectoral fin rays	×	×	
Number of dorsal fin rays	×	×	
Number of anal fin rays		×	

The mean vertebral counts for Karaginskii pinks and Kodiak-Cook Inlet pinks were 69.20 and 68.37, respectively, and their mean numbers of dorsal fin rays were 15.08 and 14.84, respectively, the Karaginskii pinks showing a larger mean value in both cases. The variance of the vertebral count is only five to six and the errors involved in counting vertebrae are small. Hence a difference in the mean value nearly as large as 1.0 is an indication that this is a very important character for separating these two groups of pink salmon.

Pearson (1963) used two meristic characters (number of vertebrae and number of branchiostegal rays) with four scale characters to distinguish between Asian and North American types of pink salmon.

Methods of analysis used for distinguishing stocks

Japanese workers, in their scale studies for distinguishing stocks, drew conclusions from comparison of mean values and frequency distributions. United States workers have used the method of distance function and discriminant function in comparing scale and meristic characters. The method of distance function in which multi-variate differences between populations are reduced to one-dimensional quantities, is effective in determining to which of known populations an unknown population is most closely related. There are no particular difficulties in constructing mathematical models by this method and in applying these models to actual data. However, in the case of the discriminant function there are some problems as to the validity of basic assumptions when this method is applied to actual data. The main question is whether or not a sample of unknown origin consists only of individuals from the populations that are chosen as morphotypes.

Amos *et al.* (1963) used the method of discriminant function to actually estimate the proportions of Asian and North American pink salmon in high seas samples. Karaginskii pinks were chosen as the Asian morphotype. Analyses were made for samples collected in 1957, when East Kamchatkan pink populations were extremely large. Hence, northern-western Alaskan pinks that might have been present in small proportions would not have been detected by this method, even if their morphological characteristics were considerably different from East Kamchatkan pinks. For this reason, Kodiak-Cook Inlet pinks, whose area of offshore distribution is contiguous with that of East Kamchatkan pinks and whose populations are large, were chosen as the North American morphotype rather than northern-western Alaskan pinks. In this case, northern-western Alaskan pinks (including Aleutian Island pinks) in offshore samples would be classified as being of Karaginskii rather than North American origin. By choosing the morphotypes as mentioned above, West Kamchatkan pinks would be classified as fish of Karaginskii origin, and southeastern Alaskan and British Columbian pinks as fish of Kodiak-Cook Inlet origin.

A mathematical requirement for discriminant function analyses is that both of the morphotypes chosen have a multivariate normal distribution and a common dispersion matrix. This assumption was satisfied in the above case.

High seas distribution of pink salmon of various origins

In order to determine the extent of intermingling of Asian and North American pink salmon on the high seas, we have to know, first of all, the populations contributing to pink salmon concentrations found in offshore waters. Then, if we can determine the proportions of individuals from different populations in such offshore concentrations, including seasonal and year-to-year variations therein, we will have achieved our objective. Sampling and analysis have been carried out more or less having this in mind for the years 1955 to 1959. Both sampling and analysis were most comprehensive in 1957, followed by 1959.

Information obtained for 1955

The results of the distance function analysis of scale measurements for samples collected from the Okhotsk Sea mothership fishery and the North American coast are shown in Table 7 (Pacific Salmon Investigations, 1958b). Among North American pink salmon, those from Attu Island showed the smallest value of distance function (D) relative to Okhotsk Sea pinks ($D=1.1$, α (error of misclassification) $=29$ percent) followed by Cook Inlet pinks ($D=1.5$, $\alpha=23$ percent). Pink salmon in areas southward from Petersburg were almost completely separate from Okhotsk pinks, the value of D being 3.6 or larger.

TABLE 7. Comparison of D and α values between Okhotsk Sea and other mainland areas for 1955–1957 (Pacific Salmon Investigations (1958 b), Table 1).

	D values			α values		
	1955	1956	1957	1955	1956	1957
Yubetsu River	—	—	2.9	—	—	7
North Kamchatka	—	—	.6	—	—	49
Attu	1.1	1.4	.9	29	24	33
Chignik	—	—	1.7	—	—	20
Unalaska	—	1.9	—	—	17	—
Adak	—	1.8	—	—	18	—
King Cove	—	1.4	—	—	24	—
Unalakleet	—	1.0	1.4	—	31	24
Kodiak	—	—	1.5	—	—	23
Cook Inlet (Seldovia)	1.5	1.7	1.7	23	20	20
Yakutat	—	1.2	—	—	27	—
Petersburg	3.6	1.5	1.4	4	23	24
Ketchikan	4.3[1]	3.3	3.4	3[1]	5	2
Nass River		3.2	4.1		5	2
Skeena River	—	3.8	3.8	—	3	3
Rivers Inlet	—	4.9	—	—	1	—
Fraser River	5.0	—	5.3	1	—	<1
LaConner, Wash.	5.3	—	—	<1	—	—

[1] Ketchikan and Nass River samples combined in 1955 analysis.

All but one of the samples collected by the Japanese mothership fishery from Aleutian waters and areas off the east coast of Kamchatka were closer to Okhotsk Sea samples than the North American samples were. A sample collected at 50°N, 162°E on August 10 resembled the Cook Inlet sample ($D=0.44$, $\alpha=41$ percent) and did not resemble any other coastal samples.

The values of D calculated from meristic characters for pink salmon samples obtained from the North American coast and the high seas in 1955 are shown in Figure 27 (Pacific Salmon Investigations, 1958c).

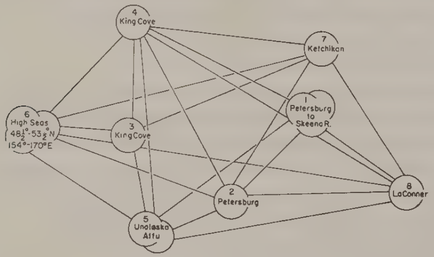


FIGURE 27. Generalized distance chart for 1955 pink salmon samples (Pacific Salmon Investigations, 1958c, Fig. 1).

The high seas samples collected from May 18 to August 10 between 154°E and 170°E and between 48°30′N and 53°30′N closely resembled the Okhotsk Sea samples and were included in one cluster (6). Pinks from LaConner (Washington), British Columbia, and southeastern Alaska (clusters 1, 2, 7, and 8) were far from Asian pinks in the model. Pinks from Unalaska, Attu, and King Cove (clusters 3, 4, and 5) were in intermediate positions. The relationships between D values calculated from meristic characters were more or less similar to those between D values calculated from scale characteristics for pink salmon samples collected in 1955.

In discriminant function analysis of scale characters, most of the high seas samples from western Aleutian waters were classified as pinks of Asian origin and most of the samples from the Gulf of Alaska as pinks of North American origin (Pacific Salmon Investigations, 1958b).

Information obtained for 1956

The D values obtained by distance function analysis of scale characters for samples collected from the Okhotsk Sea mothership fishery and the Asian and North American coasts in 1956 showed results more or less similar to those obtained for 1955 (Table 7). The value of D between Okhotsk Sea pinks and Petersburg pinks, however, decreased to 1.5 in 1956 from 3.6 in 1955.

More coastal samples were obtained in 1956 than in 1955. There were three high seas samples from the western North Pacific: one from western Aleutian waters (on July 15 at 51°50′N, 172°30′E) and two from off southeast Kamchatka (on June 15 at 46°40′N, 166°29′E and on August 5 at 49°21′N, 159°23′E). The sample from the western Aleutian waters closely resembled the Okhotsk Sea samples in scale characters ($D=0.7$, $\alpha=37$ percent). One of the two samples from off southeast Kamchatka closely resembled Unalakleet pinks ($D=0.4$, $\alpha=43$ percent), but also resembled Okhotsk Sea pinks ($D=0.6$, $\alpha=39$ percent). The other sample from off southeast Kamchatka resembled Petersburg-Yakutat pinks ($D=0.8$, $\alpha=34$ percent). This indicates the presence of North American pinks or the presence of Asian pinks whose scale characters were different from those in the Okhotsk Sea samples. The Okhotsk Sea samples were collected during the period June 21-July 13, which was earlier than the period of sampling for pinks from waters off southeast Kamchatka.

Figure 28 shows mean circulus counts in the first-year zone and those within a distance of 0.5 mm outward from the annulus for 1956 coastal and offshore samples (from Ishida and Miyaguchi, 1959b). In these mean values, high seas samples from the Okhotsk Sea and off southeast Kamchatka are more similar to Petersburg pinks than to western-central Alaskan pinks in spite of being at a greater geographical distance from the former area.

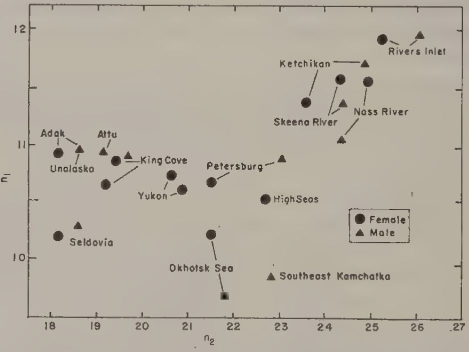


FIGURE 28. Mean values of n_1 (circuli number in the first year of growth) and n_2 (number of circuli in the distance of 0.5 mm outside of annulus). From pink salmon samples of 1956 collections. (Ishida and Miyaguchi, 1959b, Fig. 7.)

Figure 29 shows results of distance function analysis using meristic characters (Pacific Salmon Investigations, 1958c). The results are very similar to those for 1955. As in 1955, the Asian samples (clusters 9 and 10) and the British Columbian and southeastern Alaskan samples (clusters 1, 12, and 13) are situated

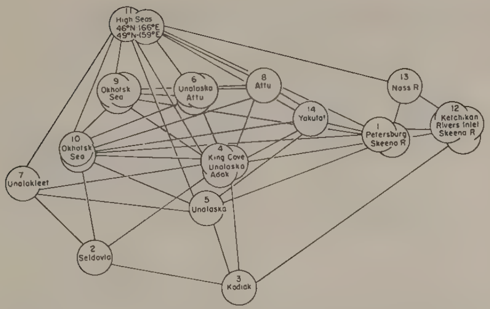

11 High Seas 46°N 166°E 49°N 159°E
9 Okhotsk Sea
6 Unalaska Attu
8 Attu
13 Nass R
14 Yakutat
12 Ketchikan Rivers Inlet Skeena R
1 Petersburg Skeena R
10 Okhotsk Sea
4 King Cove Unalaska Adak
7 Unalakleet
5 Unalaska
2 Seldovia
3 Kodiak

FIGURE 29. Generalized distance chart for 1956 pink salmon samples (Pacific Salmon Investigations, 1958b, Fig. 3).

at two extremes. The samples from Unalaska, Attu, and King Cove (clusters 4, 5, 6, and 8) are situated in between, and so are the samples from new areas —Adak, Kodiak, and Yakutat (clusters 3, 4, and 14). Pinks from Seldovia and Unalakleet (clusters 2 and 7), however, resembled Okhotsk Sea pinks.

Information obtained for 1957

The values of *D* obtained from distance function analysis of scale characters for samples collected from the high seas of the Okhotsk Sea and the Asian and North American coastal areas are shown in Table 7 (Pacific Salmon Investigations, 1958b). Karaginskii pinks most closely resembled Okhotsk pinks ($D=0.6$, $\alpha=49$ percent). The value of *D* was 0.9 between pinks from Attu and those from the Okhotsk Sea. The value of *D* was 1.0–1.9 between central-western Alaskan pinks and Okhotsk Sea pinks. Pinks taken in high seas waters off the Karaginskii district (57°N, 167°E and 58°N, 166°E) were presumably fish of East Kamchatkan origin, but the *D* values between these fish and pinks from Kodiak (0.6), Attu (0.9) and the Okhotsk Sea (0.7) were close to each other. Figures 30 and 31 show the relationships, in terms of *D* and α, between the high seas samples and the samples from the two Asian districts and the North American samples most closely resembling the high seas samples. Figure 30 shows the relationships for the high seas samples collected before July 6 and Figure 31 for those after July 10. In general, all high seas samples showed smaller *D* values with Asian samples than with North American samples. Some of them, however, showed approximately equal *D* values with

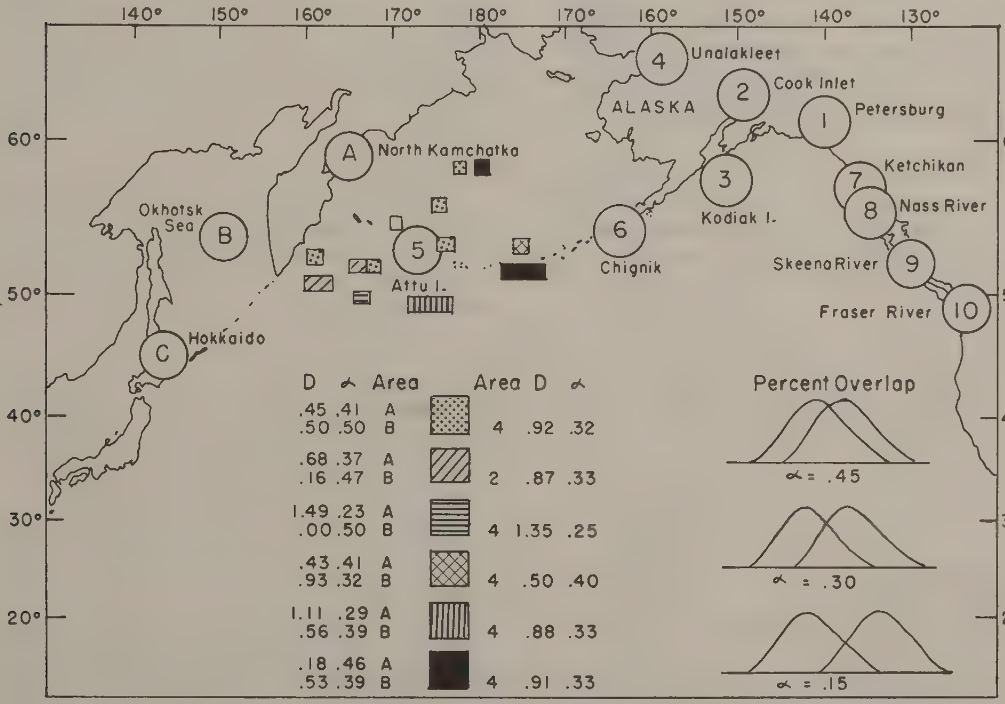

140° 150° 160° 170° 180° 170° 160° 150° 140° 130°
60° 50° 40° 30° 20°
4 Unalakleet
2 Cook Inlet
ALASKA
1 Petersburg
A North Kamchatka
3 Kodiak I.
7 Ketchikan
8 Nass River
Okhotsk Sea B
5 Attu I.
6 Chignik
Skeena River 9
Fraser River 10
C Hokkaido
D α Area Area D α
.45 .41 A .50 .50 B 4 .92 .32
.68 .37 A .16 .47 B 2 .87 .33
1.49 .23 A .00 .50 B 4 1.35 .25
.43 .41 A .93 .32 B 4 .50 .40
1.11 .29 A .56 .39 B 4 .88 .33
.18 .46 A .53 .39 B 4 .91 .33
Percent Overlap
α = .45
α = .30
α = .15

FIGURE 30. Scale analysis of 1957 pink salmon samples on the high seas between June 1 and July 6 showing racial difference (*D*) of Asian and North American areas (Pacific Salmon Investigations, 1958b, Fig. 2).

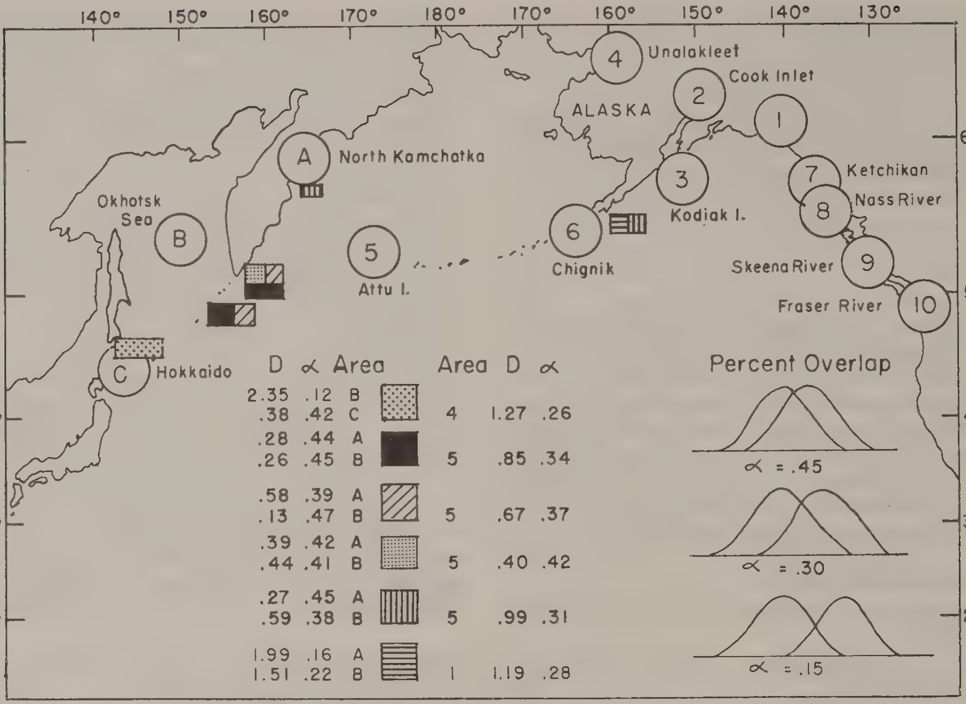

140° 150° 160° 170° 180° 170° 160° 150° 140° 130°
60° 50° 40° 30° 20°
4 Unalakleet
2 Cook Inlet
1
ALASKA
A North Kamchatka
7 Ketchikan
8 Nass River
3 Kodiak I.
Okhotsk Sea
B
5 Attu I.
6 Chignik
Skeena River 9
Fraser River 10
C Hokkaido
D α Area
Area D α
Percent Overlap
2.35 .12 B
.38 .42 C
4 1.27 .26
.28 .44 A
.26 .45 B
5 .85 .34
.58 .39 A
.13 .47 B
5 .67 .37
.39 .42 A
.44 .41 B
5 .40 .42
.27 .45 A
.59 .38 B
5 .99 .31
1.99 .16 A
1.51 .22 B
1 1.19 .28
α = .45
α = .30
α = .15

FIGURE 31. Scale analysis of 1957 pink salmon sampled on the high seas between July 10 and August 31 and near Hokkaido in September and October showing racial difference (D) of Asian and North American areas (Pacific Salmon Investigations, 1958b, Fig. 3).

North American pinks and with Karaginskii pinks. Figure 30 indicates that pink salmon found in Aleutian waters and the Bering Sea more closely resembled Karaginskii pinks than pinks from waters off southeast Kamchatka and the Okhotsk Sea.

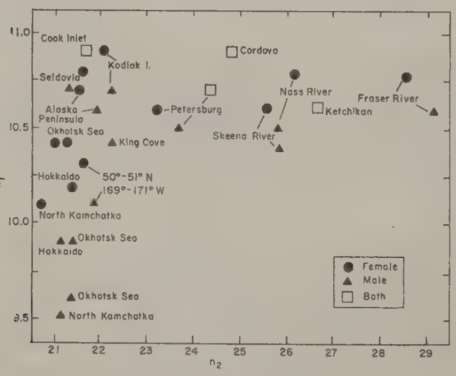


FIGURE 32. Mean values of n_1 (circuli number in the first (year of growth) and n_2 (number of circuli in the distance of 0.5 mm outside of annulus). From pink salmon scales of 1957 samples. (Ishida and Miyaguchi, 1959b, Fig. 8.)

In the number of circuli in the first-year zone, as observed by Ishida and Miyaguchi (1959b), the pink salmon samples collected in 1957 from the Okhotsk Sea, Aleutian waters and central-western Alaska did not show significant differences (Fig. 32). The number of circuli in a distance of 0.5 mm outward from the annulus, however, tended to be smaller for Asian pinks, although it varied considerably even within Asia. Samples collected by research vessels at 50°-51°N, 169°-171°W during June resembled those collected in the Okhotsk Sea and western Bering Sea, but they also resembled pinks from King Cove.

Figure 33 summarizes the results of distance function analysis of meristic characters (Pacific Salmon Investigations, 1958c). The relationships between coastal samples are more or less similar to those observed in 1955 and 1956. British Columbia samples were situated farthest from western Alaskan and Asian pinks. The greatest D value among the samples examined was between the Fraser River (cluster 20) and Unalakleet (cluster 4); the value of D was 5.4, indicating complete morphological separation.

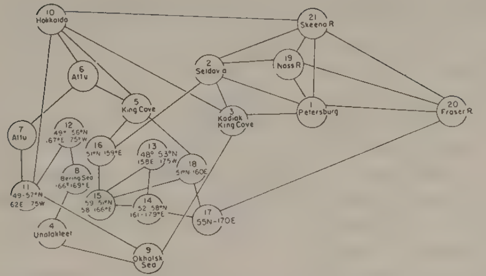


FIGURE 33. Generalized distance chart for 1957 pink salmon samples using meristic characters (Pacific Salmon Investigations, 1958c, Fig. 3).

All high seas samples (clusters 8, 11, 12, 13, 14, 15, 16, 17, and 18) closely resembled Okhotsk Sea pinks (cluster 9). However, they also resembled pinks from Unalakleet (cluster 4), Attu Island (clusters 6 and 7) and King Cove (cluster 5). The combining of scale characters with meristic characters in distance function analysis did not greatly improve the separation (Pacific Salmon Investigations, 1958a).

Table 8 shows D values between coastal samples. Asian and North American pinks are fairly well separated. The smallest D values between Asian and North American samples were 0.6 between Okhotsk Sea pinks (sample 38) and pinks from Nicholas Lake on Attu Island (sample 8), and 0.6 between Karaginskii pinks (samples 22 and 23) and King Cove pinks (sample 5). There were also a few D values smaller than 1.0 between Okhotsk Sea and Karaginskii pinks, on the one hand, and Attu, Unalakleet and King Cove pinks on the other.

Table 9 shows D values between high seas samples and samples from King Cove, Okhotsk Sea and Karaginskii. The sampling locations for high seas samples are shown in Figure 34. Judging from D values, 21 out of the 26 high seas samples showed resemblance to Asian pinks. Among these 21 samples, sample 27 also resembled King Cove pinks.

Sample 34 collected off southeast Kamchatka resembled pinks from Attu Island. Samples 13, 16, 17, and 24 (from an area of 49°–52°N, 167°–179°E on June 10, June 1, June 8, and July 1, respectively) from the northwest Pacific did not resemble any of the coastal samples.

Among the 21 high seas samples resembling Asian pinks, 15 resembled Karaginskii pinks and eight resembled Okhotsk pinks (some resembled both). Ten out of the 15 samples resembling Karaginskii pinks were taken from Aleutian waters and the Bering Sea and the remaining five were from waters off southeast Kamchatka. In contrast, seven out of the eight samples resembling Okhotsk Sea pinks were collected in waters off southeast Kamchatka and the remaining one was from the Bering Sea east of 180°.

Amos *et al.* (1963) attempted to determine the continental origin of high seas pinks collected in 1957 by discriminant function analysis of meristic and scale characters. The results are summarized in Figure 35.

They used Karaginskii and Kodiak-Cook Inlet pinks as the Asian and North American morphotypes, respectively. The characters used were the total number of vertebrae, number of dorsal fin rays and intermediate scale length.

TABLE 8. D values between North American and Asian 1957 pink salmon samples using meristic and scale characters (Pacific Salmon Investigations (1958 a), Table 3).

		Okhotsk Sea			North Kamchatka		Hokkaido			
North American area		(36)	(37)	(38)	(22)	(23)	(39)	(40)	(41)	(42)
Petersburg	(1)[1]	3.6	3.2	3.2	3.1	3.1	4.7	3.1	4.5	4.7
Seldovia	(2)	2.6	2.1	2.2	1.5	1.5	3.2	2.8	3.2	3.2
Kodiak I.	(3)	2.6	2.1	2.1	1.7	1.5	3.3	2.8	3.2	3.3
Unalakleet	(4)	1.4	1.6	1.7	.9	1.6	2.0	1.7	1.9	2.0
King Cove	(5)	1.3	.8	.9	.6	.6	2.8	2.3	2.8	2.7
King Cove	(6)	2.9	2.4	2.6	2.5	2.2	4.4	3.9	4.4	4.4
Attu I.–Gravel Pit	(7)	2.1	1.4	1.3	1.6	1.4	3.7	3.2	3.8	3.6
Attu I.–Lake Nicholas	(8)	1.5	.8	.6	1.1	1.0	3.4	2.9	3.5	3.3
Attu I.–Lake Cornica	(9)	1.9	1.3	1.2	1.4	1.2	3.7	3.2	3.8	3.6
Nass River	(45)	5.0	4.8	4.7	4.6	4.6	5.4	4.9	4.2	5.5
Fraser River	(46)	7.5	7.3	7.2	7.3	7.2	7.7	7.3	7.5	7.8
Skeena River	(47)	4.7	4.5	4.4	4.4	4.4	4.2	4.7	4.9	4.3

[1] Numbers in brackets are sample reference numbers. For position, see Figure 34.

Note: When $D=0$, there is complete similarity.
$D=4$, there is complete separation,
probability of misclassification being .02.

TABLE 9. List of D values comparing high seas samples with North American area of King Cove and with Asian areas of Okhotsk Sea and North Kamchatka using meristic and scale characters, 1957 pink salmon collections. For positions corresponding to sample number, see Figure 34 (Pacific Salmon Investigations (1958 a), Table 4).

Sample number	King Cove	Okhotsk Sea			North Kamchatka	
	5	36	37	38	22	23
10	1.0	1.3	1.0	1.2	.1*	.9
11	.8	1.2	.9	1.1	0*	.6
12	.7	1.1	.7	.9	0*	.6
13	.9	.9	.9	1.1	.8	1.2
14	.8	1.1	.8	1.1	0*	.6
15	.7	1.1	.8	1.0	0*	.3
16	1.3	.8	1.1	1.3	1.1	1.5
17	.8	.8	.8	1.0	.7	1.2
18	.7	1.1	.7	.9	0*	0*
19	1.1	1.1	.8	.9	.1*	.8
20	.9	1.3	1.2	1.2	0*	.9
21	.5	1.2	.8	1.1	.5	0*
24	1.0	.7	.6	1.0	.6	.8
25	1.0	.8	.3*	.3*	.9	1.3
26	.7	1.0	.3*	.5	.2*	.9
27	0*	.8	0*	.2	.2	.3
28	.9	.7	0*	0*	.7	1.0
29	.4	1.1	.6	.8	0*	.3
30	.6	.7	0*	.4	.9	.8
31	.8	.8	.6	.7	.1*	.9
32	.6	.9	$\underline{.3}$	$\underline{.4}$	$\underline{.3}$	.7
33	.3	1.1	.3	.7	0*	0*
34[1]	.4	1.3	.5	.7	.6	.3
35	.7	1.0	$\underline{.3}$	.5	.7	.8
43	.7	1.1	1.0	1.1	.1*	1.0
44	1.5	$\underline{.4}$	1.0	1.2	1.4	1.6

[1] $D = 0$ with Attu I.–Lake Nicholas.

* Denotes complete similarity.

— Underlined figure denotes probable origin.

Pink salmon samples from known coastal areas were tested by the discriminant function used. In Figure 35, the proportions of pinks in these coastal samples that were classified as Kodiak-Cook Inlet pinks are shown in percentage. The mean value of the discriminant Y was 85.239 for Karaginskii pinks, 83.866 for Kodiak-Cook Inlet pinks, and 84.553 for samples taken from intermediate areas. The value of Y for Okhotsk Sea pinks was greater than that for Karaginskii pinks, and the values for samples from areas eastward from Prince William Sound were smaller than that for Kodiak-Cook Inlet pinks. This means that Okhotsk Sea pinks and pinks from areas east of Prince William Sound would be classified as Asian and North American pinks, respectively. However, the mean Y values for samples from Attu Island, Unalakleet and King Cove were larger than 84.553. Accordingly, pinks belonging to the populations of these areas would be misclassified as fish of Asian origin.

The variance of discriminant function, usually expressed as D^2, was 1.373 between the two morphotypes used, indicating that the probability of individuals being correctly classified to their morphotype is approximately 72 percent. The probabilities of misclassification are that approximately 30 percent of Karaginskii pinks were classified as Kodiak-Cook Inlet pinks and 30 percent of Kodiak-Cook Inlet pinks as Karaginskii pinks.

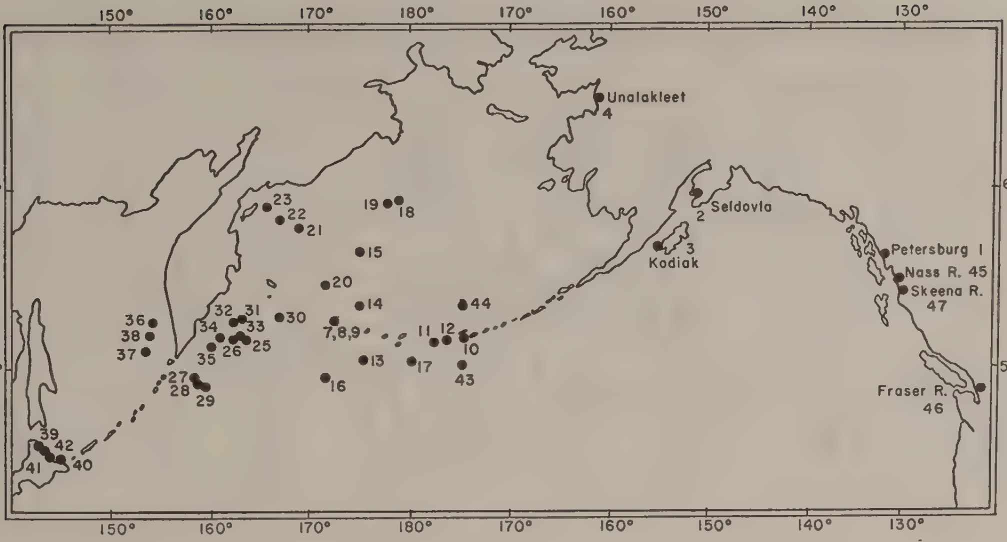
The results of classification of high seas samples by this method are shown in Figure 35. There is little evidence that the high seas samples taken from waters west of 175°W belonged to the Kodiak-Cook Inlet morphotype. Between 6 and 36 percent of the individuals in these samples were classified as the Kodiak-Cook Inlet type. Comparing these proportions with the expected probability of misclassification (28 percent) for Karaginskii pinks, even the highest observed proportion of the Kodiak-Cook Inlet type among these samples is hardly more than expected sampling errors. These high seas samples from waters west of 175°W were collected during June and July, when pink salmon abundance was extremely high in this region, and no samples were taken from this region after the abundance had decreased. The research vessel *Attu* caught 13 pink salmon at 53°40′N, 165°W on July 25, of which 10 were classified as of North American origin. No samples were collected from this vicinity at earlier dates, and it is not known what pink salmon populations occupied this area earlier in the season. Fifty-four pinks were collected at 55°N, 145°W on July 12 and a total of 37 pinks at 55°N, 135°W on July 31 and August 1, by the research vessel *Key West II*, and these samples were classified as North American fish.

Information obtained for 1958

The abundance of pink salmon in Aleutian and Bering Sea waters in 1958 was extremely low. Few high seas samples were collected, and there was little analysis. The mean circulus counts in the first year zone for coastal and high seas samples collected in this year are shown in Table 5.

Information obtained for 1959

The year 1959 was again featured by high abundance of East Kamchatkan pinks, and many high seas samples were collected from Aleutian and Bering Sea waters during June and July. Ishida (1961) compared the circulus counts in the first-year zone of high seas samples with those of the samples obtained from the Asian and North American coasts. The frequency distribution and mean of circulus counts are


150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
Unalakleet 4
2 Seldovia
3 Kodiak
Petersburg 1
Nass R. 45
Skeena R. 47
Fraser R. 46
23
22
21
19
18
15
20
14
44
36
38
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32
31
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25
35
7,8,9
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43
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42
41
40

FIGURE 34. Sampling areas for 1957 pink salmon sample collections. Figures are sample reference numbers.

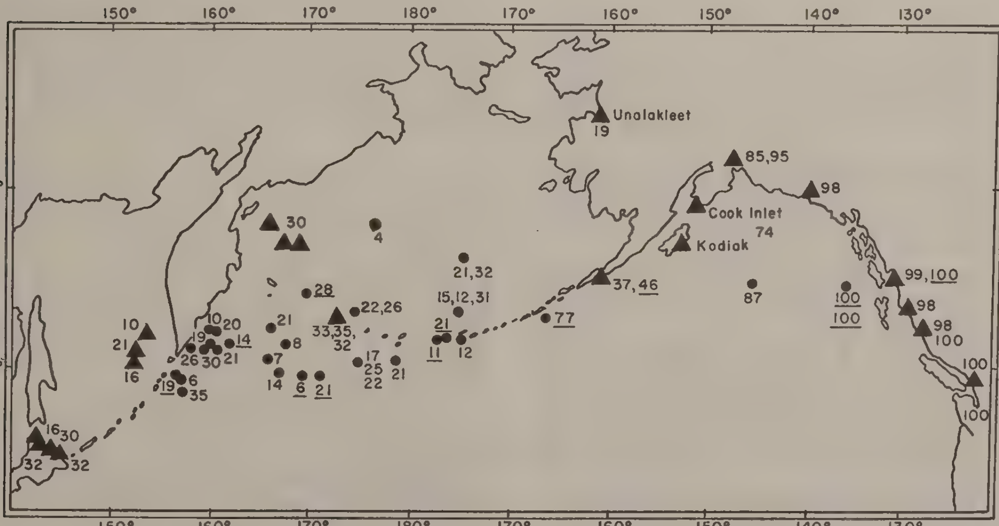
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
Unalakleet 19
85,95
98
Cook Inlet 74
Kodiak
30
4
21,32
37,46
87
100
100
99,100
28
15,12,31
77
98
22,26
98
100
10
20
21
33,35,
32
21
21
19
14
8
11
12
100
16
26
30
21
7
17
25
22
21
100
14
6
21
19
6
35
16
30
32
32

FIGURE 35. Percentage of each high seas and coastal 1957 pink salmon sample classified as being of Kodiak-Cook Inlet morphotype. Underlined figures indicate small sample sizes (less than 30 fish). (Amos *et al.*, 1963, Figs. 5 and 7.)

shown in Table 5 and Figure 36.

As seen in the figure, the mean circulus count of pinks caught by the mothership fishery in 1959 was 21.3 for the western Bering Sea, 21.4–22.0 for waters around Attu Island and the Komandorski Islands, and 20.2–21.4 for the southwestern part of the mothership fishing grounds. In contrast, the mean count of North American pinks was 24.1 for Unalakleet, 23.8 for the Alaska Peninsula and 24.0 for Kodiak Island, all being considerably larger than the mean counts for fish from the mothership fishing grounds. Compared with the mean value of 21.3 for the pinks caught

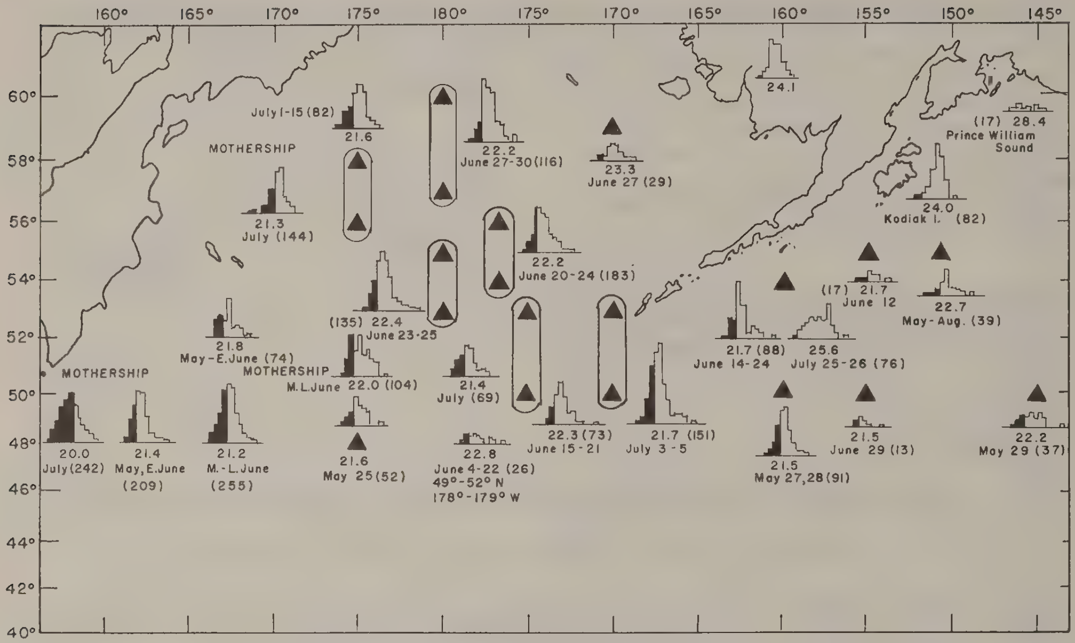
160°
165°
170°
175°
180°
175°
170°
165°
160°
155°
150°
145°
60°
58°
56°
54°
52°
50°
48°
46°
44°
42°
40°
July 1-15 (82)
21.6
MOTHERSHIP
21.3
July (144)
22.2
June 27-30 (116)
23.3
June 27 (29)
24.1
(17) 28.4
Prince William
Sound
24.0
Kodiak I. (82)
22.2
June 20-24 (183)
(135) 22.4
June 23-25
21.8
May-E.June (74)
MOTHERSHIP
M.L.June 22.0 (104)
MOTHERSHIP
21.4
July (69)
(17) 21.7
June 12
22.7
May-Aug. (39)
21.7 (88)
June 14-24
25.6
July 25-26 (76)
20.0
July (242)
21.4
May, E.June
(209)
21.2
M.-L.June
(255)
21.6
May 25 (52)
22.8
June 4-22 (26)
49°-52° N
178°-179° W
22.3 (73)
June 15-21
21.7 (151)
July 3-5
21.5
May 27,28 (91)
21.5
June 29 (13)
22.2
May 29 (37)

Figure 36. Frequency distribution and mean values of circuli in the first-year growth of North Pacific pink salmon in 1959. Figures in brackets show number of specimens. Figures under histograms show mean values. Columns in histogram smaller than 19 inclusive are shaded. (Ishida, 1961, Figs. 9 and10.)

in the western Bering Sea by the mothership fishery in July, which can safely be considered to be Karaginskii fish, the mean values for the North American samples were more than 2.5 greater.

High seas samples were collected by research vessels from all waters east of 175°E at 5° longitude intervals except along 165°W.

The mean value in circuli for the fish taken along 175°E was 21.6 at 48°N (collected May 25) and again 21.6 between 56°–58°N (collected during July 5–15). These values were very close to those for Asian pinks estimated from samples obtained from the mothership fishery.

Along 180°, fish collected from 53°–55°N during June 23–25 had a mean value of 22.4, and those collected from 57°–60°N during June 27–30 had a mean value of 22.2. These values were slightly larger than those obtained from the mothership fishery. There are two possibilities that might account for such differences. Since fish in early migrations include more males and more larger fish, they might have higher circulus counts than those in late migrations. Secondly, it is possible that some North American pinks with higher circulus counts were included. The former explanation is considered to be more likely, but the possibility of the latter cannot be excluded. The frequency distribution has an extended slope to the right, suggesting the possible presence of North American fish.

Along 175°W the fish collected from 51°–53°N during June 15–21 had a mean value of 22.3, and those collected from 54°–56°N during June 22–24 had a value of 22.2. These values were very similar to those obtained for samples from 180°.

Along 170°W the fish collected from 51°–53°N during July 3–5 had a value of 21.7, and those collected at 59°N on June 27 a value of 23.3. Fish from 51°–53°N are considered to have been of East Kamchatkan origin. Those samples taken at 59°N were presumably dominated by fish of North American origin.

Along 160°W, the pinks collected at 50°N during June 27–28 had a mean value of 21.5, those taken at 54°N during June 14–24 a value of 21.7, and those taken at 54°N during July 25–26 a value of 25.6. The fish taken during mid and late June were almost certainly East Kamchatkan pinks, as indicated by their mean value and frequency distribution. Those from 54°N in late July were apparently pinks of North American origin.

Along 155°W, small samples were collected at 50°N and 55°N during mid and late June, and their mean values were 21.5–21.7. A mean value of 22.7 was observed for fish taken at 150°W, 55°N during May-August. The pinks taken from 155°W are likely to have been East Kamchatkan pinks but their abundance was low. The value of 22.7 observed at 150°W is greater than the mean value for East Kamchatkan pinks but still lower than the lowest mean value for North American coastal samples. In 1959, Cook Inlet samples were missing in the samples taken from the North American coast. As seen in Table 5, pinks in this district tended to have the smallest circulus count in the first-year zone among North American fish. Consequently, it is possible that the above pinks taken at 150°W were actually Cook Inlet fish. Alternatively Asian fish might have been present.

Summary

Since 1955, United States and Japanese research workers have attempted to distinguish Asian and North American pink salmon by using differences in various scale and meristic characters.

Both scale and meristic characters are useful for distinguishing continental stocks. Their effectiveness, however, varies considerably from time to time and from area to area. The main characteristics used were the number of vertebrae, number of dorsal fin rays, number of circuli in the first-year zone and spacing of circuli near the center of scales.

The methods used for analysis include distance function, discriminant function, and comparison of mean values and frequency distributions. Regardless of the method of analysis used, the main difficulty was the lack of large differences in racial characters between East Kamchatkan pinks and pinks in areas west and north of the Alaska Peninsula, which are the two most important groups of pinks involved in intermingling. Also, when the proportion of one or the other group was small in high seas samples, it was not possible either to confirm or deny the presence of fish belonging to such a group, because the proportion is within the limits of error. Nevertheless, these racial studies resulted in many valuable findings.

EVIDENCE FROM OTHER SOURCES

Certain inferences concerning the origin of pink salmon in offshore waters can be drawn from examination of catch and effort and from biological data. The evidence is very general in nature and is not conclusive for the identification of the major stocks of Asian and North American pinks and their migratory pattern. However, it does supplement the observations in the preceding sections.

Coincidence of fluctuations in abundance in coastal and high seas waters

Relatively larger concentrations of pink salmon occur in Bering Sea and Aleutian waters in years when large pink catches are made in East Kamchatka than in years when East Kamchatkan pink catches are low. The year-to-year fluctuations in abundance of pink salmon in waters of the Bering Sea and off the Aleutian Islands, as reflected by the relative abundance indices of the INPFC research vessels and Japanese motherships, have generally coincided with the fluctuations in the coastal catch of East Kamchatkan pink salmon (Table 10). For the odd-numbered years of 1955, 1957 and 1959 the relative abundance indices of the research vessels are more closely associated with the East Kamchatkan coastal catch than those of the motherships, while the reverse is true in the even-numbered years of 1956, 1958 and 1960. These associations between coastal catch and abundance of pink salmon in offshore waters seem to suggest that perhaps pink salmon found in Bering Sea and Aleutian waters at this time of the year are predominantly of East Kamchatkan origin.

TABLE 10. Bering Sea-Aleutian area relative abundance indices of INPFC research vessels and Japanese motherships and the East Kamchatkan coastal catch for the years 1955–1960.

Year	Relative abundance index: Research vessels	Relative abundance index: Motherships	East Kamchatkan coastal catch (metric tons)
1955	6.0	.95	12,500
1956	.9	.08	500
1957	19.8	3.43	22,300
1958	.9	.17	1,700
1959	11.8	4.12	18,000
1960	2.5	.22	4,700

During the years 1955–1958 the period of best mothership catches (per tan) in the Okhotsk Sea varied (Fig. 37). The late June and early July catches were very small in 1956 and the middle and late July catches were very small in 1958. The coastal catches of pink salmon in West Kamchatka and the Okhotsk district are shown in Table 11. It is noticed that in 1956 the coastal catch in the Okhotsk district was small and the early-season mothership catch was also small, while in 1958 the coastal catch in West Kamchatka was small and the late-season mothership catch was also small. The fishing season is earlier in the Okhotsk district than in West Kamchatka, although the former district is higher in latitude than the latter (Kaganovski, 1949; Taguchi, 1957). From these observations it may be inferred that pink salmon contributing to the

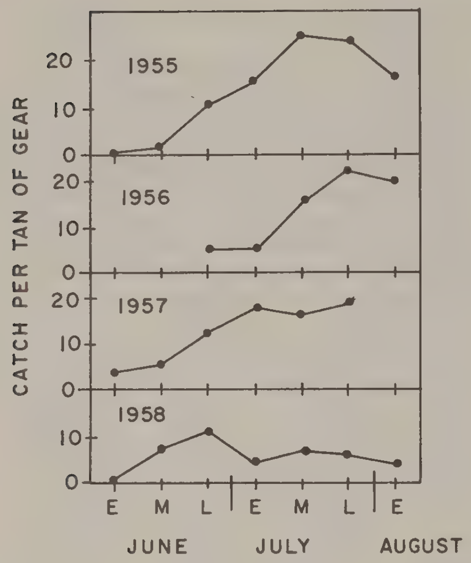

Figure 37. Seasonal change of pink salmon catch per tan of gear in Okhotsk Sea mothership fishery, 1955–1958.

Table 11. Comparison of coastal pink salmon catch in West Kamchatka and Okhotsk districts (1000's of metric tons).

Year	West Kamchatka	Okhotsk
1955	41.4	19.1
1956	27.6	1.1
1957	53.1	17.3
1958	1.3	3.8
1959	8.8	7.3
1960	1.9	3.6

Table 12. Annual changes in average lengths of pink salmon of Primore, Amur River, and west coast of Hokkaido in 1957–1960.

Area and year	June		July	
	Male	Female	Male	Female
Primore				
1957	47.9		51.3	
1958	42.9	43.9	46.2	44.6
1959	53.6	49.8	56.2	51.2
1960			51.4	48.1
Amur				
1957	46.2		47.9	
1958	40.6	41.8	43.2	41.7
1959	48.7	46.6	51.0	48.3
1960	46.9	44.8	47.8	44.9
Off west coast of Hokkaido	*Late April-May*			
1958	41.7	40.3		
1959	44.6	42.8		
1960	42.4	41.8		

earlier part of the fishing season are bound for the Okhotsk district, and those contributing to the later part are bound for West Kamchatka.

Size, weight and gonad development as indicators of the offshore distribution of stocks

Birman (1956) noticed that during 1946–1949 pink salmon in Primore and on the west coast of Sakhalin were larger in size in years of high abundance (odd-numbered years in this case), thus departing from the general rule that pink salmon were smaller in years of high abundance. He suggested that the ocean habitat of these stocks coincides with that of the Amur River pink salmon in which the " on " and " off " years are the reverse of the Primore and West Sakhalin stocks. According to the statistical data on the coastal catches of the U.S.S.R. for the years 1957–1960, Primore and Amur pinks were particularly small in 1958 (Table 12). This might indicate that pinks of these two districts shared feeding grounds, and the cause of their extremely small size in 1958 could have been the unusually high abundance of Amur pinks in the same year. Pink salmon caught off the west coast of Hokkaido were also small in 1958. These observations suggest that the majority of the pinks caught off the west coast of Hokkaido are migrating to Primore, Amur and West Sakhalin areas.

Dvinin (1962) observed that in 1947 and 1949, the abundance of the spawning populations of pink salmon on the west coast of South Sakhalin was at a high level and, at the same time, the average length of pinks belonging to these populations was large. In 1946 and 1948 the abundance of the populations was at a low level and the average lengths were smaller than those of the years 1947 and 1949. Contrary to this, pink salmon from the southern part of East Sakhalin had larger average lengths in 1946, when spawning populations were small. In 1947, spawning populations were large, but average lengths were much smaller than in 1946. Lengths decreased again in 1949, when catches were high. Dvinin recognizes, in his report, that what he calls " west coast spawning populations " are not salmon bound for the adjacent coast. The catches along the Pacific coast of Hokkaido during the years 1946–1949 were 565 tons, 3,341 tons, 668 tons, and 6,658 tons, respectively, coinciding with the changes in the catches on the east coast of Sakhalin. These observations indicate that pinks bound for the east coast of South Sakhalin grow mostly in waters other than the Japan Sea.

It is interesting to speculate where these Sakhalin " west coast spawning populations " migrate for spawning. It is obvious, from the above observations, that they are not bound for East Sakhalin. It may be suspected that they consist mainly of fish migrating to the west coast of central and northern Sakhalin and to the streams of the Okhotsk districts. Odd-year runs dominated in western and eastern Sakhalin and Okhotsk districts during the period 1946–1949. The Amur district had strong even-year runs.

Additional information useful in separating Asian populations of pink salmon was provided by analysis of the length distribution of pink salmon measured aboard motherships during 1957–1960. In Figures 38 and 39 the length frequency distribution of pink salmon caught by motherships during 1957–1960 in the northwest Pacific Ocean and Bering Sea and Okhotsk Sea waters is shown by months. The distribution was corrected for the bias caused by mesh selectivity (Manzer *et al.*, 1965). The selectivity curves used for this purpose are not precise. Corrections were possible for a length range of 44–48 cm, where the selectivity of commercial mesh sizes

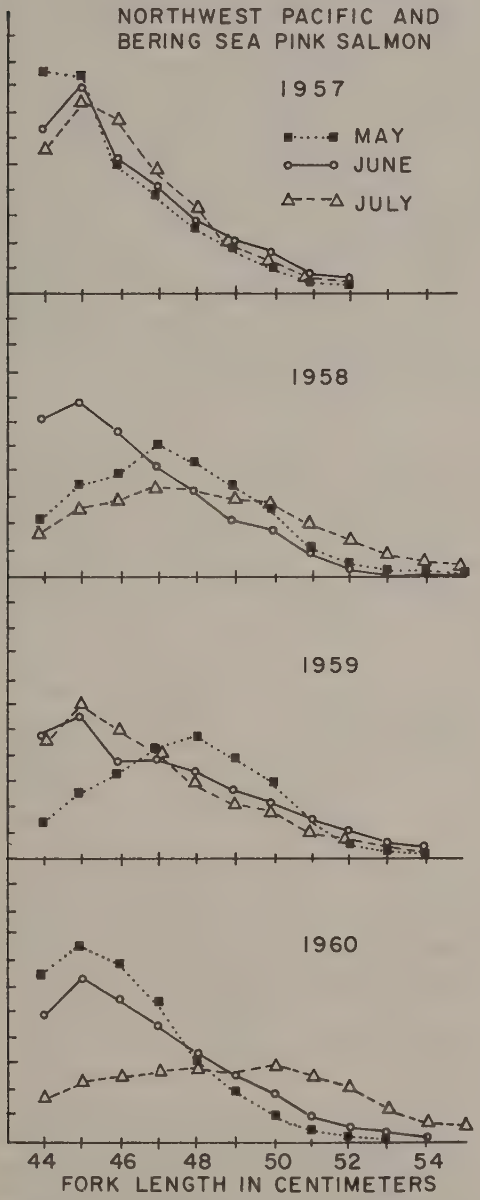

FIGURE 38. Frequency distribution of fork length of pink salmon caught by motherships in northwest Pacific and Bering Sea, 1957–1960. Adjustment to mesh selectivity was made roughly.

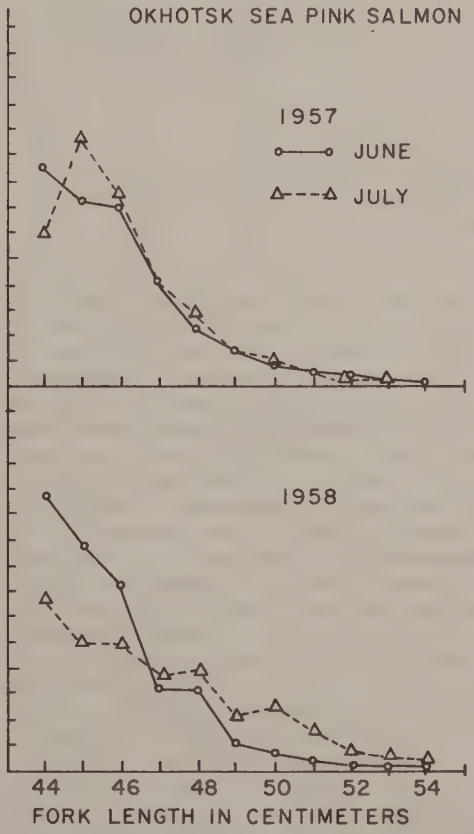

FIGURE 39. Frequency distribution of fork length of pink salmon caught by motherships in the Okhotsk Sea, 1957–1958. Adjustment to mesh selectivity was made roughly.

(12.1 cm, stretched measure) changes sharply. The combined length frequency distribution for pink salmon from North Pacific Ocean and Bering Sea waters is shown in Figure 38. The frequency distribution of pink salmon from the Okhotsk Sea is shown in Figure 39. It can be seen in Figure 38 that in 1957 the mode of length frequency distribution was 45 cm or less during the period May through July, that in 1958 the mode was at 45 cm in June and at 47 cm in May and July, and that in 1960 the mode was at 45 cm in May and June and 50 cm in July. Since corrections made by selectivity curves were only approximate, the position of modes mentioned above are not necessarily accurate. It is certain, however, that the mode varied between and within years.

In Table 13 the average lengths of pink salmon caught on the U.S.S.R. coast during 1957–1960 are shown by months. East Kamchatkan pinks were smaller than West Kamchatkan pinks in the years 1958, 1959 and 1960, the average difference being 5–6 cm. However, lengths given in this table were presumably measured after secondary sexual characteristics had developed, and therefore may not be strictly comparable. In 1957, West Kamchatkan pinks were markedly smaller than in subsequent years.

Table 13. Mean fork lengths of coastal catch of pink salmon in Kamchatka, 1957–1960 (from U.S.S.R. official data). Fork lengths in centimeters.

Date		Okhotsk	Southwest Kamchatka	Northwest Kamchatka	East Kamchatka
1957	June	45.0	46.9	—	—
	August	46.5	48.9	49.3	—
1958	June	47.8	51.5	—	45.8
	August	48.4	53.5	53.4	—
1959	June	49.0	51.9	50.5	47.3
	August	48.6	53.8	51.6	—
1960	June	—	53.1	51.7	46.4
	August	—	52.8	54.4	—

According to Figure 39, the mode of the length frequency distribution of Okhotsk Sea pinks in June and July was at 45 cm or less both in 1957 and 1958. Comparing these length frequency distributions with those for North Pacific Ocean pinks as shown in Figure 38, there was no significant difference between the two in 1957, but there was some difference in the position of the mode in 1958. Since corrections of length frequency distribution were approximate, the above comparison may merely indicate that pinks caught in the Okhotsk Sea were somewhat smaller than those caught in the Pacific Ocean. On the other hand, it is shown in Table 13 that in 1958 the average length of pink salmon caught on the coast off the Okhotsk district was 4–5 cm smaller than those of pinks caught in West Kamchatka. Hence, it might be assumed that small pink salmon caught by motherships in the Okhotsk Sea in 1958 were pinks bound for the Okhotsk district. This supports the previous suggestion that the pink salmon caught by the mothership fishery in the Okhotsk Sea during June and early July were bound for the Okhotsk district.

There is some additional information to substantiate the above. Ishida and Miyaguchi (1959b) pointed out that in 1957 there was a significant difference in body weight between pink salmon taken by the motherships in waters off the southeastern coast of the Kamchatka Peninsula and those taken by motherships in the Okhotsk Sea, although there was little difference in length between the two. The average weight was 1.28 kg in June and 1.39 kg in July for the former, and 1.11 kg in June and 1.13 kg in July for the latter. The average weight of pinks in the coastal catches of the U.S.S.R. in the same year was 1.28 kg in July and 1.38 kg in August for West Kamchatkan pinks (Bolshaia River), and 1.17 kg in July and 1.15 kg in August for Okhotsk district pinks. The average body length, however, was about 2 cm greater for the former than for the latter. In the mothership catch in the Okhotsk Sea during 1957, the proportion of pink salmon belonging to the earlier peak was still high even in July. These facts indicate that the majority of the pink salmon caught by the Okhotsk Sea mothership fishery in June and early July were Okhotsk district

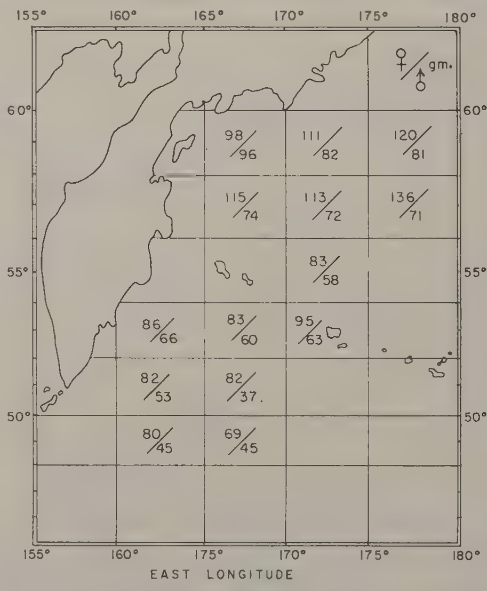

Figure 40. Average gonad weights of high seas pink salmon caught by motherships in early July of 1959.

pinks and that at least in 1957 most of the pink salmon found in the southwestern part of the mothership fishing grounds of the northwest Pacific Ocean during June and July were West Kamchatkan pinks.

Kaganovski (1949) and Taguchi (1957) state that the peak of the coastal fishing season of Oliutorskii-Karaginskii pinks was from mid-July to late July and that in West Kamchatka the peak of pink fishing was in late July and runs continued until late August. In Figure 40, the average gonad weights of pink salmon caught by motherships in Aleutian and Bering Sea waters during early July 1959 are shown by regions. Those caught in Bering Sea waters had gonads about 30 g heavier for both sexes than those from waters off southeastern Kamchatka, reflecting the above difference in timing of coastal migration. A reasonable interpretation would be that the pinks caught in the Bering Sea were migrating to the Oliutorskii-Karaginskii region and those caught in the waters off southeastern Kamchatka to West Kamchatka.

Parasitological and serological studies

The possibility of using parasites in pink salmon as a means of distinguishing between Asian and American stocks has been investigated (INPFC, 1958). Although more than 30 species of helminth parasites were identified in the samples none was restricted to pink salmon taken in waters adjacent to one or the other of the two continents and at the same time sufficiently abundant and widespread to be useful. Mamaev *et al.* (1959) in their study of the internal parasite fauna of the Far Eastern salmon, including pinks, found some differences in the parasitization of salmon from different Asian areas but since their work was preliminary no definite conclusions can be drawn.

Ridgway and Klontz (1961) in their work on the serology of Pacific salmon found evidence for the existence of blood group differences in pink salmon and a single difference was noted which appeared to be correlated with the area of origin of sample but no practical method which can be applied in clarifying the distribution of pink salmon stocks has been found.

MINGLING OF STOCKS IN OFFSHORE WATERS

In the sense in which the term " stock " has been used in this report—namely for the fish which can be associated with a large, more or less well-defined coastal region—it is evident that no stock has an ocean distribution which is at all times separate from the territory occupied by one or more other stocks. " Intermingling " or " mixing " of course implies association in time as well as in space, but how close these associations should be in order to qualify for these terms is a matter of definition. Although in some instances fish caught in the same " set " have been found to proceed subsequently to quite different coastal regions, thus showing very close association between certain individuals of presumably different stocks, this report in general uses these terms in the sense of an overlapping in the areas occupied by pink salmon of different origin as shown by fish caught within a time period of not more than a few weeks.

Without etymological basis but in deference to a usage which has been frequent in INPFC investigations, the term " intermingling " is used here in relation to the overlapping of Asian and American stocks. " Mixing " is used to describe the association between stocks originating on or near the same continent.

Mixing of stocks having a common continent of origin

In the sense of the foregoing remarks tagging experiments have shown a mixing of stocks from Primore and Sakhalin Island in the Sea of Japan in April and May of odd and even years, with Amur River pink salmon also present in even years. (It is interesting to note that, as mentioned in the section " Evidence from other sources ", a common ocean feeding ground for Amur, Primore and West Sakhalin pink salmon was postulated previously on the basis of differences in the average size of some of these fish in different years.)

Taggings have also shown that fish which proceeded to widely separated coastal areas of the Okhotsk Sea (Sakhalin Island, Hokkaido, northern Okhotsk coast and West Kamchatka) were present in a common ocean area east of the Kurils in June 1959.

On the North American side tagging records show that Norton Sound and Bristol Bay pinks were both present along much of the Aleutian chain in June 1958 and in certain eastern parts of the same region in June 1960. An overlapping distribution of these stocks in Aleutian waters was also evident in June 1961. Furthermore, fish of both these stocks were present in June 1958 on the south side of the Alaska Peninsula coincidentally with fish bound for spawning areas within the Gulf of Alaska.

As shown especially by the tagging program of 1962, there is extensive overlapping in the ocean distribution of the main stocks of pink salmon originating in the Gulf of Alaska.

Intermingling between Asian and American stocks

Information on the overlapping of ocean distribution between fish originating in Asia and North America is largely confined to the Aleutian region and involves mainly pink salmon breeding in the East

Kamchatka-Oliutorskii region on the one hand and western Alaska on the other. Tag recoveries show a total recorded overlap (irrespective of year and season) extending from 177°E to 155°W, i.e., 28 degrees of longitude or about 1000 miles (1600 km) in an east-west direction at this latitude. However, owing to the existence during the period of investigations of large fluctuations in the abundance of East Kamchatkan stocks and a relatively low level of abundance of Alaskan stocks in this region, the extent of intermingling which has been demonstrated for any given month of a given year is small. Thus, no North American recoveries of fish tagged within the above noted area of overlap were made in 1957 or 1959 and no Kamchatkan fish were recovered in 1958.

In June 1960 a Kamchatka-bound fish and an Alaska-bound fish were each tagged at about 172°W. In June 1961 an Alaskan fish was tagged as far west as 176°W and an Asian fish was tagged as far east as 164°W, thus indicating an overlap of 12 degrees of longitude. In June 1962 fish of both continents were present at about 168°W.

It may be noted that direct tagging evidence of intermingling is confined to the month of June. Taggings conducted in July show no overlapping in the distribution within any one year, the fish presumably being mostly segregated and en route to their respective destinations by this time of year. One Asian fish tagged on July 3, 1961, and one Bristol Bay fish tagged on July 1, 1958, were close to the same position near Adak (176°W–178°W). Tagging experiments conducted prior to June have been so scanty as to provide very little information on the areas occupied by Asian and western Alaskan stocks at this season. However, recoveries in 1957 of fish tagged on May 27 as far east as Unimak Island (four from the East Kamchatkan coast and three from intermediate high seas localities) indicate the probability of extensive intermingling of these stocks in some years and the near certainty that some East Kamchatkan pinks are at times in close proximity to populations originating in drainage areas of the Gulf of Alaska.

The evidence on the distribution of Asian and American pink salmon provided by scale and meristic studies and by consideration of the year-to-year abundance of fish in coastal waters is in general conformity with the results of tagging experiments.

In 1955, 1956 and 1958 the number and geographic distribution of the high seas samples obtained were insuffcent to permit interpretation of the areas occupied by the fish of each continent. In 1957 these studies indicated that the pink salmon found in high concentrations in waters west of 175°W during June and July were bound for streams in the Karaginskii district or areas farther westward. However, the possibility of very small quantities of northwestern Alaskan pinks being present in this region cannot be excluded, since these fish resembled Karaginskii pinks in the characters used. Also, it is not known what populations occupied this region after the sampled populations had left. No samples were taken during May and June in waters east of 175°W and it is therefore impossible to say anything about the distribution of pinks in this region early in the season. Samples taken in late July consisted of fish of North American origin, as were salmon collected from the Gulf of Alaska east of 145°W.

In 1959 there were considerable differences in the circulus counts of the first year zone between Asian and North American pinks and, since widespread sampling was carried out, the situation was favorable for determining the origin of high seas fish through scale studies. Pink salmon found in high concentrations in Aleutian and Bering Sea waters during June and early July and those found in Gulf of Alaska waters at 155°W and 160°W until late June were presumably East Kamchatkan fish. Pink salmon presumably bound for northwestern Alaska were found in the northeastern part of the Bering Sea (59°N, 170°W) in late June. North American pinks apparently predominated also in the vicinity of 160°W during July and later.

The indicated presence of Kamchatkan fish at 155°W in 1959 represented an extension of the range of Asian fish beyond that which had been shown at that time by tagging experiments. Recent tagging supports this conclusion. In the opposite direction, it is obvious that the tag recoveries do not show the westward limits of those American pink salmon which breed in the Aleutian Islands to as far west as Attu Island (173°E).

Within the large region in which fish of both continents occur at times, there is great variation in the numbers and proportions present, not only from year to year but also at different seasons within a year. It is not possible to describe a meaningful " average situation ". The chief factor in the variation, during the period of investigations, has been the fluctuation in abundance of the East Kamchatkan stocks. To a considerable extent this fluctuation has been between " even " and " odd " years. However, there can be no assurance that the pattern of fluctuations so far observed (which in itself is not entirely consistent) will be maintained in the future. It is well known that " dominance " of an even- or odd-year line has sometimes been reversed, and of course marked changes in the absolute numbers of either or both lines can occur without necessarily involving a reversal of " dominance ".

Under these circumstances it is only possible to present conclusions that can be reached for individual years of the INPFC investigations. It should be remembered, too, that the evidence applies only to a very limited season of the year.

For 1955 and 1956 there are insufficient data to justify any quantitative comparisons between Asian and American fish.

In 1957 Asian fish predominated in the Aleutian region in May and June from 173°E to 164°W.

In 1958 American fish were present (in relatively small numbers) in the Aleutian region westward to 177°E in June and July. No Asian fish were shown to be present east of 175°E.

In 1959 Asian fish predominated in the Aleutian region in June and early July eastward to 168°W and probably, in June, to 155°W in the Gulf of Alaska. The presence of American fish was not shown in these regions during this period but they predominated in a sample taken in late June in the northeast Bering Sea at 170°W and, in late July, at 160°W in the Gulf of Alaska.

In 1960 Asian fish were probably present in the Aleutian region to 164°W and predominant to at least 178°W in May and June. American fish were present to at least 173°W in June and July.

In 1961 Asian fish were present in the Aleutian region to 164°W and predominant to 170°W in June. American fish were not shown to be present in the region until July (at 169°W).

In 1962 American fish predominated in June at 166°–168°W in the Aleutian region. However, a tag recovery from Karaginskii showed that some Asian fish were present in the same area.

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Seasonal Movements of Striped Bass, *Roccus saxatilis* (Walbaum), Tagged and Released in the Potomac River, Maryland, 1959–61

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Seasonal Movements of Striped Bass, *Roccus saxatilis* (Walbaum), Tagged and Released in the Potomac River, Maryland, 1959–61[1]

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ABSTRACT: During 1959–61, 8,973 striped bass, *Roccus saxatilis* (Walbaum), were tagged and released in the Potomac River, Maryland. Of the 3,344 (37.3%) recaptured, 98.0% were taken in the Maryland part of Chesapeake Bay and its tributaries, 0.5% were recovered in the Virginia part of Chesapeake Bay and its tributaries, and 1.5% were taken outside Chesapeake Bay along the Atlantic coast from Delaware to Nova Scotia. In the wintering season (November–March), the tagged fish were concentrated in the lower river and were very active, traveling several miles a day. In the spawning season (April–June), they mostly moved upstream to the spawning grounds where the tagged fish remained for most of the season, and then dispersed downstream to the lower river and into Chesapeake Bay. In the feeding season (July–October), tagged fish were scattered throughout Chesapeake Bay and tributaries. Some striped bass which overwintered in the Potomac were recaptured during the following spawning season in other Chesapeake Bay tributaries, and fish from the Potomac contributed materially to the stocks of striped bass along the northeast Atlantic coast. Spawning striped bass return to the same spawning grounds in successive years. Recaptures of tagged fish by date and location during the wintering, spawning, and feeding seasons, and the miles traveled and days at large by individuals, are tabulated.

Introduction

Migration of striped bass, *Roccus saxatilis* (Walbaum), is extremely variable. Merriman (1941: 33–46) and Raney (1952: 19–30) reported a mass migration of fish to the north along the Atlantic seaboard in late winter and early spring and to the south in the fall and early winter. Chapoton and Sykes (1961: 18–19), Hollis and Davis (1955: 2), Mansueti (1956: 4–6; 1958: 22; and 1961: 9–36), Pearson (1933: 15–17; and 1938: 842–844), and Vladykov and Wallace (1938: 67–86; and 1952: 163–175) published pertinent information on movements of striped bass in Chesapeake Bay. These workers reported that most recaptures of fish tagged and released within the bay were made in the general vicinity of the release site. Some fish, however, traveled relatively great distances within the bay and a few were recaptured outside the bay. They reported that larger striped bass moved greater distances, on the average, than smaller individuals. Massmann and Pacheco (1961: 39–41), who studied movements of striped bass in Virginia tributaries of Chesapeake Bay, reported that

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94% of all tagged fish recaptured were taken from the river system in which they were tagged.

Although striped bass are anadromous, various size and age groups are present year-around in the Potomac River because of favorable spawning, nursery, feeding, and wintering areas. Spawning takes place from April to June throughout the river from upper Cedar Point to Whitestone Point, a distance of about 30 miles. Males 2 or more years old and females 4 or more years old make up the spawning stock.

The striped bass is the most valuable commercial and sport fish in the Potomac River. The average annual commercial catch of about 1 million pounds is composed mainly of 2-, 3-, and 4-year-old fish. The sport catch is substantial but unrecorded. The fisheries depend largely upon congregations of migrating striped bass; therefore, knowledge of the seasonal movements is of value in management as well as to fishermen.

This paper contributes information about the seasonal movements of striped bass tagged and released in the Potomac River, Maryland, 1959–61 (Fig. 1).

The tagging project reported in this paper was part of a cooperative study among the Maryland Department of Research and Education,[4] the Virginia Institute of Marine Science, and the Bureau of Commercial Fisheries. This paper summarizes only a part of the data from the cooperative research; data used in the analyses also have provided the basis for estimates of the population and utilization rates.

Collection, Age Determination, Tagging, and Tag Recovery

During 1959–61, we tagged and released a total of 8,973 striped bass: 6,197 in the wintering season, 1,854 in the spawning season, and 922 in the feeding season (Table 1). Seasons of release or recapture were based on the species' activity in Maryland as: wintering season, November-March, when most fish are congregated in a somewhat inactive condition in the deeper waters of Chesapeake Bay and lower tributaries; spawning season, April–June, when mature fish are in fresh or slightly brackish tidal waters; and feeding season (months of heavy feeding and growth), July–October, when most fish are schooled in the open waters of the bay. The tagging was distributed throughout the river, both below and on the spawning grounds.

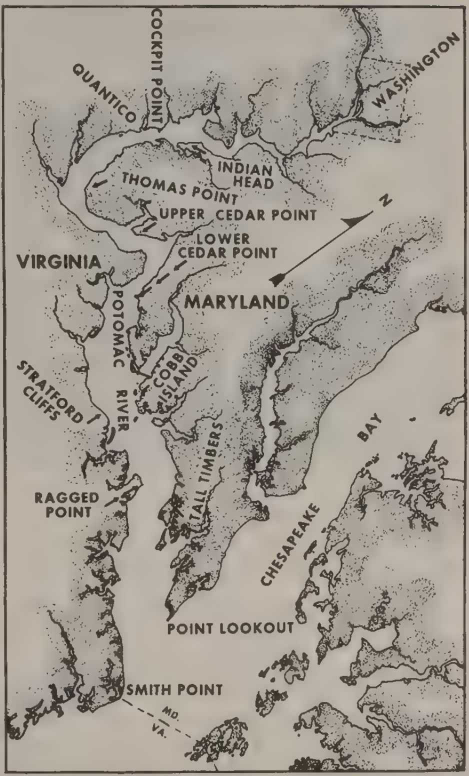

Fig. 1. Map of the Potomac River, Maryland.

The fork length of each fish tagged was measured to the nearest 0.1 inch (Table 1). More than 60% of the tagged fish were 10 to 17 inches long.

When possible, mature fish were sexed by manually extruding sex products. As indicated by Raney (1952: 31) and Sykes (1958: 104), however, sex determination of live striped bass, other than ripe males, is extremely difficult. Consequently, many males were identified during the spawning

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TABLE 1. Tagging summary for striped bass released during the wintering, spawning, and feeding seasons, Potomac River, Maryland, 1959–61.

Year	Season	Date released	Number tagged fish released	Collecting gear	Release site	River mile	Range in fork length in inches	Range in age
1959	Wintering	Jan. 21–30	633	Trawl	Lower Cedar Point, Maryland, to Quantico, Virginia	42–68	8.3–28.6	1–6
		Feb. 2–3	106	Trawl	Upper Cedar Point, Maryland, to Thomas Point, Maryland	50–59	8.8–17.8	1–4
		Mar. 16–30	706	Stake gill net	Blake Creek, Maryland, to Cockpit Point, Virginia	20–70	10.2–30.4	1–9
	Spawning	Apr. 3–30	473	Stake gill and pound nets	Ragged Point, Virginia, to Indian Head, Maryland	20–75	9.4–44.0	1–15
		May 1–15	276	Stake gill and pound nets and haul seine	Piney Point, Maryland, to Quantico, Virginia	16–68	7.9–46.5	1–19
	Feeding	Oct. 27–30	922	Pound net	Stratford Cliffs, Virginia, to Potomac Beach, Virginia	30–39	9.3–19.0	1–5
1959–60	Wintering	Nov. 2–13	472	Pound net	Stratford Cliffs, Virginia, to Sandy Point, Maryland	30–66	8.4–18.4	1–5
		Mar. 2–31	2,073	Stake gill net	Tall Timbers, Maryland, to Blue Bay, Maryland	18–64	8.5–36.1	1–11
1960	Spawning	Apr. 1–29	444	Stake gill and pound nets	Cobb Island, Maryland, to Quantico, Virginia	33–68	10–1–46.0	1–18
		May 3–6	187	Stake gill net	Sandy Point, Maryland, to Quantico, Virginia	66–68	11.1–31.2	1–11
1960–61	Wintering	Mar. 1–23	2,207	Stake gill net	Tall Timbers, Maryland, Potomac Creek, Virginia	18–58	9.0–31.3	1–14
1961	Spawning	Apr. 25–27	474	Stake gill and pound nets	Sandy Point, Maryland, Quantico, Virginia	66–68	11.0–42.5	1–16

season, but few females were identified in any season.

Age of tagged fish was determined by examination of scales taken above the lateral line between the two dorsal fins. Fish collected during the spawning and feeding seasons were aged by counting the annular rings laid down on the scale, according to the method described by Scofield (1931: 26) and Merriman (1941: 23–25). Thus, a three-ring scale taken from a fish during the spawning or feeding season indicates an age of 3 years. Fish taken during the wintering season, when growth ceases before annulus formation, were advanced 1 year. Thus, a fish caught during the wintering season with a three-ring scale was designated as 4 years old. Fish tagged during the wintering season were 1 to 16 years old; about 86% were 2 or 3 years old. Fish tagged during the spawning season were 1 to 19 years old; about 60% were 2 or 3 years old. Fish tagged during the feeding season were 1 to 5 years old, and about 95% were 2 or 3 years old.

Fish were marked with a streamer tag with a 7-inch loop of nylon net twine. The loop was threaded through the back of the fish under the second dorsal fin (Fig. 2 and 3) with a 7-inch upholsterer's needle having a notched eye. The twine was knotted securely so that the tag trailed over the caudal peduncle. One side of the tag carried a code number and the other a return address and reward notice. Tagging techniques were similar to those used on striped bass by Davis (1959: 319) and Lewis (1961: 4).

Several methods were employed to recover tags. Biologists canvassed fishermen in the field for recaptured tags and distributed self-addressed, postage-paid envelopes for returning tags. Similar envelopes were included with letters to fishermen explaining our tagging program, and with letters acknowledging returned tags. Newspaper articles explaining our tagging study furthered tag returns in areas where sport and commercial fishermen were concentrated. A reward of $1.00 was paid for each tag returned.

Nature of the Recaptures

Of the 8,973 striped bass tagged and released, 3,345, or 37.3%, were recaptured (Table 2). Of those recaptured 3,276 (98.0%) were taken in the Maryland part of Chesapeake Bay and tributaries, 17 (0.5%) in the Virginia part of Chesapeake Bay and tributaries, and 52 (1.5%) outside Chesapeake Bay. Recaptures of tagged fish by season and month, location, distance from the release site, and days at large are given in Tables 3–9.

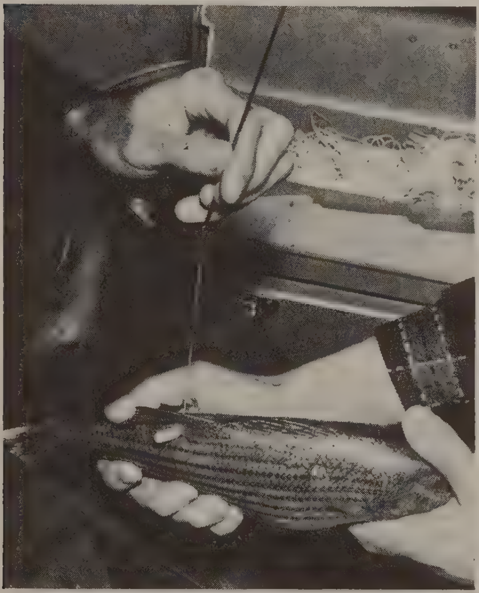

Fig. 2. Affixing nylon streamer tag to a striped bass.

Fig. 3. Two striped bass caught in drift gill net. Note: The fish on the right is tagged with a nylon streamer tag.

The 6,197 striped bass tagged and released during the wintering season (November–March) yielded 2,618 recaptures. Of those recaptured, 2,369 (90.5%) were taken in the Potomac—1,791 below the spawning area and 578 in the spawning area; 190 (7.3%) in the Maryland part of Chesapeake Bay and tributaries other than the Potomac; 16 (0.6%) in the Virginia part of Chesapeake Bay and tributaries; and 43 (1.6%) outside Chesapeake Bay and in tributaries from Delaware Bay to Nova Scotia, Canada (Tables 2, 3, 6, and 8).

The 1,854 striped bass tagged and released during the spawning season (April–June) provided 555 recaptures, of which 480 (86.5%) were taken in the Potomac, 67 (12.0%) in the Maryland part of Chesapeake Bay and tributaries other than the Potomac, 1 (0.2%) in the Virginia part of Chesapeake Bay, and 7 (1.3%) outside Chesapeake Bay from Long Island, New York, to Nova Scotia (Tables 2, 4, 7, and 9).

The 922 striped bass tagged and released during the feeding season (July–October) gave 172 recaptures: 163 (94.5%) were taken in the Potomac, 7 (4.3%) in the Maryland part of Chesapeake Bay, and 2

TABLE 2. Summary of recaptures from 8,973 striped bass tagged and released during the wintering, spawning, and feeding seasons, Potomac River, Maryland, 1959–61.

Releases		Area of recaptures								
		Maryland				Virginia				
		Potomac River		Chesapeake Bay		Chesapeake Bay				
Season and year	Tagged fish	Spawning grounds	Below spawning grounds	Tributaries other than Potomac	Bay proper	Tributaries	Bay proper	Outside Chesapeake Bay	Total	
Wintering:										
1959.........	1,445	151	249	—	22	1	3	4	430	29.8
1959–60......	2,545	224	679	12	83	—	2	19	1,019	40.0
1960–61......	2,207	203	863	13	60	8	2	20	1,169	53.0
Subtotal	6,197	578	1,791	25	165	9	7	43	2,618	42.3
Spawning:										
1959.........	749	60	71	1	22	—	—	3	157	21.0
1960.........	631	117	89	1	21	—	—	4	232	36.8
1961.........	474	117	26	1	21	—	1	—	166	35.0
Subtotal	1,854	294	186	3	64	—	1	7	555	29.9
Feeding:										
1959.........	922	10	153	—	7	—	—	2	172	18.6
Subtotal	922	10	153	—	7	—	—	2	172	18.6
TOTAL	8,973	882	2,130	28	236	9	8	52	3,345	37.3

(1.2%) outside Chesapeake Bay off Rhode Island and Maine (Tables 2 and 5).

Movements of Tagged Striped Bass

The recaptures of tagged striped bass clearly were affected by season and location of fishing effort and therefore did not necessarily indicate where the majority of tagged fish were located at any one time. Also, no information was available to show how extensive the movements of the tagged fish may have been between release and recapture. All movements indicated by the recaptures should be accepted with these reservations in mind.

SEASONAL MOVEMENT

The seasonal movements were similar, with some exceptions, to the general movements first outlined by Vladykov and Wallace (1938: 67–86 and 1952: 164–175) and recently described by Whitney (1961: 35), Massmann and Pacheco (1961: 37–44), and Mansueti (1961: 17–33) for striped bass caught and tagged in the Maryland part of Chesapeake Bay. The findings of these several authors indicated the following seasonal pattern of movement: (a) spawning season—general upstream movement to the tributaries and in the bay (small, presumably immature, females remained at the tagging site); (b) feeding season—general dispersal downstream into the bay and river mouths and some interchange between estuaries, but also with some individuals remaining at the tagging site; and (c) wintering season—concentration in the deeper waters of the tributaries and bay where the fish made minor but definite movements for short distances. The principal differences between our findings and those of the above workers were that some of our tagged fish traveled several miles during the wintering season, and we found considerable movement out of the river in the late part of the wintering season and early part of the spawning season.

Recaptures by season of striped bass

Table 3. Recaptures by month during the wintering, spawning, and feeding seasons from 1,445 striped bass, tagged and released during the wintering season, January–March 1959, Potomac River, Maryland [See Table 1 for release data].

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1959										
Wintering										
Feb.	Maryland, Potomac River:									
	Below spawning grounds	8	16	1–25	22	10–32	3	2–3	14.4	9.8–17.1
	Maryland, Chesapeake Bay:									
	Off South River	1	112	—	33	—	3	—	14.6	—
Mar.	Maryland, Potomac River:									
	Spawning grounds	38	8	0–14	26	0–63	2	2–3	14.5	12.3–18.5
	Below spawning grounds	91	10	0–46	24	0–68	2	2–4	14.9	9.5–19.0
	Maryland, Chesapeake Bay:									
	Kent County, Eastern Shore	1	120	—	11	—	3	—	16.0	—
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	93	19	0–46	39	5–94	3	2–4	16.2	12.5–20.8
	Below spawning grounds	90	13	0–48	40	34–95	3	2–6	14.6	9.9–28.6
	Maryland, Chesapeake Bay:									
	North Black to mouth Gunpowder River	5	118	91–145	24	15–31	3	—	14.9	13.9–16.4
	Virginia, Chesapeake Bay:									
	Near James River Bridge	2	112	—	9	8–11	3	—	15.3	14.9–15.7
	Virginia, Rappahannock River:									
	Off Morattico, Lancaster County	1	70	—	13	—	2	—	13.2	—
	Delaware, Delaware Bay:									
	Off Ship John Shoal Light	1	190	—	20	—	3	—	17.8	—
May	Maryland, Potomac River:									
	Spawning grounds	3	25	19–30	71	51–107	2	2–3	12.4	9.5–16.2
	Below spawning grounds	6	19	18–20	76	57–120	2	2–3	12.1	9.4–16.2
June	Maryland, Potomac River:									
	Spawning grounds	1	11	—	129	—	2	—	11.5	—
	Below spawning grounds	6	20	11–32	137	130–146	2	2–4	14.0	11.5–17.8
	Maryland, Chesapeake Bay:									
	Off Cedar Point, St. Marys County	1	63	—	99	—	3	—	15.7	—
Feeding										
July	Maryland, Potomac River:									
	Spawning grounds	1	20	—	108	—	3	—	14.6	—
	Below spawning grounds	6	14	11–17	147	110–166	2	2–3	12.3	10.9–14.1
	Maryland, Chesapeake Bay:									
	Chesapeake Beach to Susquehanna Flats	3	127	107–151	170	164–177	3	2–3	15.3	13.5–17.1
Aug.	Maryland, Potomac River:									
	Below spawning grounds	3	14	1–23	201	196–209	2	2–3	12.4	10.1–14.6
	Maryland, Chesapeake Bay:									
	Poplar Island and off Rock Hall	2	106	93–120	138	132–144	3	—	15.6	13.9–17.4
Sept.	Maryland, Potomac River:									
	Below spawning grounds	2	15	7–24	196	191–201	2	—	10.0	9.8–10.3
	Maryland, Chesapeake Bay:									
	Mouth Choptank River to off Rock Hall	3	95	84–105	197	175–224	—	2–3–8	19.4	14.2–29.5
	Nova Scotia, Bay of Fundy:									
	Near Walton Light House	1	1,270	—	159	—	3	—	17.6	—
Oct.	Maryland, Potomac River:									
	Below spawning grounds	5	17	1–37	256	201–279	2	2–3	12.7	9.2–16.5
	Maryland, Chesapeake Bay:									
	Off Millers Island	1	110	—	254	—	2	—	14.1	—
1959–60										
Wintering										
Nov.	Maryland, Potomac River:									
	Below spawning grounds	3	9	6–12	239	233–245	3	2–3	13.3	9.9–15.2
Jan.	Virginia, Chesapeake Bay:									
	Hampton Roads Area	1	100	—	288	—	3	—	15.7	—
Mar.	Maryland, Potomac River:									
	Spawning grounds	1	12	—	360	—	3	—	14.7	—
	Below spawning grounds	11	13	3–25	373	341–421	3	2–4	14.2	9.2–16.6
1960										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	13	18	0–31	404	384–447	3	2–8	16.1	9.3–28.2
	Below spawning grounds	12	10	3–25	388	367–435	3	2–3	14.4	9.9–17.4
	Maryland, Chesapeake Bay:									
	Chesapeake and Delaware Canal	1	200	—	458	—	2	—	12.0	—
May	Rhode Island, Atlantic Ocean:									
	Off Sakonet Point	1	526	—	446	—	2	—	11.1	—
Feeding										
Aug.	Maryland, Chesapeake Bay:									
	Near Sandy Point	1	143	—	473	—	3	—	17.5	—
	New York, Atlantic Ocean:									
	Off Long Island	1	410	—	500	—	3	—	17.4	—

TABLE 3—*Continued*

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1960–61										
Wintering										
Mar.	Maryland, Potomac River:									
	Below spawning grounds	3	14	12–18	706	705–708	2	2–3	13.8	12.8–14.8
1961										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	1	20	—	761	—	3	—	14.9	—
	Below spawning grounds	2	24	14–24	758	747–769	3	—	16.0	14.2–17.2
Feeding										
Aug.	Maryland, Potomac River:									
	Below spawning grounds	1	19	—	868	—	3	—	15.4	—
	Maryland, Chesapeake Bay:									
	Kent Narrows and off Rock Hall	2	112	105–120	864	861–868	3	—	15.8	14.7–16.8
1963										
Feeding										
Oct.	Maryland, Chesapeake Bay:									
	Near Bay Bridge	1	88	—	1,621	—	5	—	24.6	—

tagged and released during the wintering, spawning, and feeding seasons are given in Table 10.

MOVEMENT OF STRIPED BASS TAGGED DURING THE WINTERING SEASON

As was previously stated, the tagged fish were highly active in the wintering season and traveled as much as several miles a day. The minimum distances traveled by tagged fish recaptured within the wintering season of release ranged from 0 to 275 miles (average, 8 miles). The length of time that the recaptured fish were free ranged from 0 to 144 days (average, 9½ days). One fish tagged in January was recaptured in Chesapeake Bay 112 miles from the tagging site 33 days after release, and another, tagged in November, was recaptured off the New Jersey coast 275 miles from the release site 8 days later. How much effect tagging had on the migrations of these fish cannot be determined. Some individual migrations not in keeping with the general pattern suggested, however, that tagging may have stimulated some fish to move.

Within the season of release, several tagged fish were recaptured in waters other than the Potomac River: 10 in the Maryland part of Chesapeake Bay and other tributaries, 4 in the Virginia part of Chesapeake Bay and tributaries, and 1 in Great Egg Harbor, New Jersey.

Recaptures in the latter part of the wintering season and early part of the following spawning season indicated a general movement upstream to the spawning area, principally in April, of the fish tagged in the lower river. Of the 4,205 fish tagged and released in the lower river, only 8% of the 755 recaptures in March, but 56% of the 563 recaptures in April, were made in the spawning area.

Several fish tagged during the wintering season were recaptured in Chesapeake Bay tributaries other than the Potomac during the early part of the following spawning season. For example, 20 tagged fish were recaptured in April in the Nanticoke, Patuxent, Little Choptank, Blackwater, Gunpowder, Choptank, and Chester Rivers in Maryland, and 6 were caught in the Rappahannock and Piankatank Rivers, Virginia.

Recaptures in the following seasons indicated a general dispersal of the tagged fish; a large portion of the recoveries were in the Maryland part of Chesapeake Bay.

MOVEMENT OF STRIPED BASS TAGGED DURING THE SPAWNING SEASON

Recoveries of striped bass tagged during the spawning season indicated that most of the tagged fish moved into the spawning

TABLE 4. Recaptures by month during the spawning, feeding, and wintering seasons from 749 striped bass tagged and released during the spawning season, April–May 1959, Potomac River, Maryland. [See Table 1 for release data].

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1959										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	28	12	0–19	4	0–19	3	2–5	15.6	12.9–20.0
	Below spawning grounds	15	10	4–27	8	0–22	3	2–7	15.9	13.2–31.1
May	Maryland, Potomac River:									
	Spawning grounds	8	15	0–44	9	0–32	2	2–7	17.7	10.8–30.1
	Below spawning grounds	8	13	0–38	8	3–14	2	2–7	14.2	9.8–33.3
June	Maryland, Potomac River:									
	Below spawning grounds	9	12	2–27	48	26–77	2	2–3	12.2	9.1–14.3
	Maryland, Chesapeake Bay:									
	Eastern Bay	1	95	—	58	—	6	—	30.8	—
	Massachusetts, Buzzards Bay:									
	Off Cuttyhunk	1	575	—	68	—	10	—	37.3	—
Feeding										
July	Maryland, Potomac River:									
	Spawning grounds	2	37	36–38	56	53–58	2	2–2	11.4	10.6–12.3
	Below spawning grounds	2	12	7–16	55	54–56	2	2–2	11.4	10.4–12.4
	Maryland, Chesapeake Bay:									
	Eastern Bay to off Rock Hall	3	112	80–148	90	73–99	—	4–5–6	26.4	23.9–29.5
Aug.	Maryland, Potomac River:									
	Below spawning grounds	3	21	4–27	103	97–106	2	2–2	12.3	10.8–13.3
	Maryland, Chesapeake Bay:									
	Eastern Bay–Love Pt.	2	115	90–140	121	119–123	3	3–3	16.3	16.2–16.4
Sept.	Maryland, Potomac River:									
	Below spawning grounds	2	12	2–25	139	138–140	—	2–4	17.7	12.9–22.5
	Maryland, Chesapeake Bay:									
	Off Calvert Co., to Northeast River	7	129	65–185	144	114–168	3	2–8	24.2	14.0–33.6
Oct.	Maryland, Potomac River:									
	Below spawning grounds	2	2	0–4	157	155–159	—	2–3	13.3	10.6–15.9
	Maryland, Chesapeake Bay:									
	Off Worton Point	2	162	162–162	165	161–169	4	4–4	21.9	19.9–23.9
	New York, Atlantic Ocean:									
	Off Montauk, Long Island	1	470	—	183	—	8	—	33.0	—
1959–60										
Wintering										
Nov.	Maryland, Potomac River:									
	Spawning grounds	2	31	27–36	186	186–187	2	2–2	13.4	12.2–14.7
	Below spawning grounds	2	11	7–15	166	161–171	—	2–3	12.8	11.6–14.0
Dec.	Maryland, Potomac River:									
	Below spawning grounds	1	16	—	244	—	3	—	16.4	—
Mar.	Maryland, Potomac River:									
	Spawning grounds	1	20	—	307	—	2	—	13.1	—
	Below spawning grounds	7	22	0–41	326	299–346	2	2–3	14.3	12.9–16.6
	Maryland, Chesapeake Bay:									
	Off mouth Potomac River	1	50	—	350	—	3	—	13.1	—
1960										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	16	15	0–38	362	330–388	3	2–6	15.8	12.1–30.3
	Below spawning grounds	12	18	0–43	357	336–377	3	2–5	14.4	11.1–22.7
	Maryland, Chesapeake Bay:									
	Near Millers Island	1	118	—	364	—	4	—	22.8	—
	Maryland, Patuxent River:									
	Off Benedict, Calvert County	1	148	—	352	—	3	—	15.2	—
	New Jersey, Atlantic Ocean:									
	Off Ocean City	1	368	—	341	—	3	—	15.5	—
May	Maryland, Potomac River:									
	Spawning grounds	2	13	11–15	374	373–376	—	3–6	21.2	16.1–26.3
	Below spawning grounds	2	4	0–7	363	355–371	2	2–2	10.8	10.8–10.8
	Maryland, Chesapeake Bay:									
	Off Bohemian River mouth	1	135	—	370	—	2	—	13.0	—
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds	1	45	—	467	—	5	—	22.8	—
Oct.	Maryland, Potomac River:									
	Below spawning grounds	1	13	—	529	—	2	—	11.2	—
	Maryland, Chesapeake Bay:									
	Near Pooles Island	1	153	—	527	—	6	—	30.0	—

TABLE 4—*Continued*

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1960–61										
Wintering										
Nov.	Maryland, Potomac River: Below spawning grounds	2	31	31–31	533	525–542	2	2–2	12.7	12.0–13.4
	Maryland, Chesapeake Bay: Near Tilghman Island	1	85	—	541	—	2	—	11.7	—
Dec.	Maryland, Potomac River: Below spawning grounds	1	18	—	578	—	3	—	15.5	—
	Maryland, Chesapeake Bay: Near Cove Point	1	91	—	593	—	3	—	14.5	—
1961										
Spawning										
Apr.	Maryland, Potomac River: Spawning grounds	1	38	—	749	—	4	—	23.7	—
May	Maryland, Potomac River: Below spawning grounds	1	31	—	742	—	5	—	26.6	—
1962										
Spawning										
June	Maryland, Chesapeake Bay: Gooses area	1	111	—	1,145	—	6	—	27.8	—

area early in the season and remained in that area for most of the spawning period. In April and May, 71% of the 322 recaptures within the river were made in the spawning area, whereas in June, 12% of the 16 recaptures were made in the spawning area. Only 6 recoveries were made out of the river within the season of release and 5 of these were in June within 47 to 68 days after release. The tagged fish recaptured outside probably spawned before they left the river.

Recaptures of tagged fish during the following seasons indicated about the same movements as were demonstrated by recaptures of fish during the wintering season (Table 10).

MOVEMENT OF STRIPED BASS TAGGED DURING THE FEEDING SEASON

Recaptures of striped bass tagged during the feeding season indicated that the fish remained in the Potomac during the season of release and the following wintering season (Table 10). Within the season of release, all 25 recaptures were made in the river below the spawning area. Of the 95 recoveries in the following wintering season, all except 3 were below the spawning area.

In the following seasons, most of the recaptures were made in the Potomac and the Maryland part of Chesapeake Bay and indicated about the same movements as were shown by captures from fish tagged during the wintering and spawning seasons.

STOCKS WINTERING IN THE POTOMAC RIVER

Some of the striped bass tagged during the wintering season in the Potomac River were recaptured within the season of release and during the following spawning season in other Chesapeake Bay tributaries. Within the season of release, 3 tagged fish were taken in other tributaries—1 below the spawning grounds in the Patuxent River, Maryland, and 1 each in spawning grounds of the Rappahannock and York Rivers, Virginia. The recoveries were made from 3 to 33 days and from 42 to 120 miles from the date and point of release. The age of these fish ranged from 2 to 4 years. Of the 26 tagged fish caught in other tributaries during the following spawning season, 24 were recaptured in April—20 in the Choptank, Little Choptank, Blackwater, Gunpowder, Patuxent, and Nanticoke Rivers, Maryland, and 4 in the Rappahannock and York Rivers, Virginia. These recaptures came 13 to 60 days after release and 65 to 98 miles from the point

TABLE 5. Recaptures by month during the feeding, wintering, and spawning seasons from 922 striped bass tagged and released during the feeding season, July–October 1959, Potomac River, Maryland. [See Table 1 for release data].

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1959										
Feeding										
Oct.	Maryland, Potomac River:									
	Below spawning grounds..........	25	2	0–9	2	1–4	1	1–2	11.8	9.9–16.2
1959–60										
Wintering										
Nov.	Maryland, Potomac River:									
	Below spawning grounds..........	64	5	0–20	13	2–35	2	1–4	12.6	10.1–19.0
Dec.	Maryland, Potomac River:									
	Spawning grounds................	1	34	—	57	—	1	—	11.8	—
	Below spawning grounds..........	17	6	0–20	39	11–56	1	1–2	12.6	9.8–16.1
Jan.	Maryland, Potomac River:									
	Below spawning grounds..........	1	15	—	64	—	1	—	11.1	—
Feb.	Maryland, Potomac River:									
	Below spawning grounds..........	1	13	—	74	—	2	—	15.4	—
Mar.	Maryland, Potomac River:									
	Spawning grounds................	2	32	31–33	122	98–141	—	1–2	15.7	10.7–17.8
	Below spawning grounds..........	9	6	0–10	125	104–143	—	2–2	15.8	15.5–16.1
1960										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds................	6	27	20–38	136	127–144	2	2–3	15.8	15.1–17.3
	Below spawning grounds..........	15	7	0–15	132	103–158	2	1–3	14.7	10.3–17.7
	Maryland, Chesapeake Bay:									
	Bay Bridge—mouth Elk River....	2	119	96–142	122	115–130	—	2–2	15.3	14.6–16.0
May	Maryland, Potomac River:									
	Spawning grounds................	1	30	—	157	—	2	—	12.6	—
	Below spawning grounds..........	6	9	4–12	174	160–179	2	1–2	12.4	10.3–17.2
	Maryland, Chesapeake Bay:									
	Buoy 18—mouth Patuxent River..	2	55	50–60	174	169–180	—	2–2	15.8	15.3–16.4
	Rhode Island, Narragansett Bay:									
	Off mouth Providence River......	1	565	—	186	—	2	—	14.2	—
June	Maine, Piscataqua River:									
	Near river mouth................	1	750	—	200	—	2	—	15.3	—
1960										
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds..........	2	4	3–6	235	233–237	—	1–2	13.0	11.2–13.8
Aug.	Maryland, Potomac River:									
	Below spawning grounds..........	1	0	—	279	—	1	—	11.0	—
	Maryland, Chesapeake Bay:									
	Gooses–Bay Bridge...............	2	83	70–96	269	267–271	2	2–2	15.4	14.7–16.1
Sept.	Maryland, Potomac River:									
	Below spawning grounds..........	2	4	3–6	326	310–342	—	2–3	12.9	11.9–14.0
Oct.	Maryland, Potomac River:									
	Below spawning grounds..........	3	7	3–12	362	347–371	2	2–3	14.7	14.1–15.9
1960–61										
Wintering										
Nov.	Maryland, Potomac River:									
	Below spawning grounds..........	2	7	0–15	389	389–389	2	2–2	15.0	14.7–15.4
Mar.	Maryland, Potomac River:									
	Below spawning grounds..........	1	12	—	473	—	2	—	16.9	—
1961										
Spawning										
May	Maryland, Potomac River:									
	Below spawning grounds..........	1	2	—	529	—	2	—	13.6	—
Feeding										
Aug.	Maryland, Chesapeake Bay:									
	Off Rock Hall....................	1	110	—	623	—	2	—	14.7	—
1961–62										
Wintering										
Dec.	Maryland, Potomac River:									
	Below spawning grounds..........	1	10	—	775	—	1	—	11.4	—
1962										
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds..........	2	0	—	626	618–634	—	1–2	13.1	10.8–15.5

of release. All these recoveries were made in or near the spawning grounds, and most of the fish were 3 or 4 years old. Since all were recaptured in or near the spawning grounds, they probably had moved from the Potomac River wintering grounds into the other tributaries to spawn. Massmann and Pacheco (1961: 37–44) reported that

TABLE 6. Recaptures by month during the wintering, spawning, and feeding seasons from 2,545 striped bass tagged and released during the wintering season, November 1959–March 1960, Potomac River, Maryland. [See Table 1 for release data].

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1959–60										
Wintering										
Nov.	Maryland, Potomac River:									
	Below spawning grounds	30	20	0–42	12	2–24	2	2–4	11.4	9.3–17.4
	Virginia, Chesapeake Bay:									
	Off Reedville	1	42	—	9	—	3	—	14.5	—
Dec.	Maryland, Potomac River:									
	Spawning grounds	1	4	—	51	—	2	—	11.2	—
	Below spawning grounds	20	28	7–42	36	22–50	2	2–3	10.2	8.8–12.0
Mar.	Maryland, Potomac River:									
	Spawning grounds	18	5	0–20	8	0–27	3	2–3	15.7	11.4–18.5
	Below spawning grounds	186	6	0–48	9	0–144	3	2–3	16.2	9.0–22.1
	Maryland, Chesapeake Bay:									
	North Beach and Rock Hall	2	101	85–117	14	11–17	3	3–3	15.3	15.2–15.4
	Virginia, Chesapeake Bay:									
	Off Hampton	1	78	—	3	—	3	—	18.3	—
	New Jersey, Atlantic Ocean:									
	Great Egg Harbor	1	275	—	8	—	3	—	17.2	—
1960										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	174	24	0–50	25	4–174	3	2–5	16.8	9.7–26.2
	Below spawning grounds	374	9	0–32	15	1–156	3	2–11	16.5	9.8–33.0
	Maryland, Chesapeake Bay:									
	Fishing Bay to mouth Elk River	11	103	46–113	34	10–175	3	2–4	16.9	10.8–20.5
	Maryland, Chesapeake Bay tributaries:									
	Little Choptank River	1	56	—	34	—	4	—	17.6	—
	Choptank R., mouth and Cambridge	2	66	61–70	26	22–29	4	3–4	17.5	17.1–17.9
	Nanticoke R., Riverton and Sharpstown	2	70	69–71	27	22–32	3–4	3–4	18.4	17.9–19.0
	Patuxent R., Nottingham District	1	75	—	15	—	4	—	17.4	—
	Chester R., mouth and Chestertown	2	110	105–115	25	18–31	4	4–4	19.0	19.0–19.1
	Blackwater R., near Robbins	1	57	—	23	—	3	—	17.9	—
	New York, Gravesend Bay:									
	The Narrows	1	345	—	17	—	3	—	18.2	—
May	Maryland, Potomac River:									
	Spawning grounds	20	24	4–44	58	32–191	3	2–4	16.1	9.8–23.5
	Below spawning grounds	25	17	3–42	104	39–206	3	2–4	14.2	8.6–19.2
	Maryland, Chesapeake Bay:									
	Chesapeake Beach to Bodkin Point	5	88	46–121	51	4–65	3	3–3	16.4	15.3–17.5
	Delaware, Delaware River:									
	Between Alloway and Hope Creeks	1	153	—	40	—	3	—	17.6	—
	Maine, Kennebec River:									
	Near river mouth	1	668	—	62	—	3	—	18.3	—
	New Jersey to Massachusetts, Atlantic Ocean:									
	Seaside Heights, New Jersey to Buzzards Bay, Massachusetts	5	480	315–565	52	38–66	3	3–3	17.3	16.5–17.7
June	Maryland, Potomac River:									
	Below spawning grounds	4	9	2–17	70	67–74	3	3–3	16.6	13.0–18.8
	Maryland, Chesapeake Bay:									
	Cove Pt. to Chester River mouth	5	81	43–125	80	72–87	3	3–3	16.7	14.1–17.5
	New York, Atlantic Ocean:									
	Off Long Island	1	427	—	106	—	3	—	17.5	—
	Massachusetts, Atlantic Ocean:									
	Cape Cod area	1	527	—	75	—	3	—	16.6	—
Feeding										
July	Maryland, Potomac River:									
	Spawning grounds	1	33	—	130	—	2	—	9.8	—
	Below spawning grounds	4	14	4–19	108	104–112	3	3–4	15.6	14.5–16.8
	Maryland, Chesapeake Bay:									
	Off Patuxent River to Rock Hall	9	97	40–130	116	94–131	3–4	2–4	17.6	13.5–20.8
	Massachusetts to Maine, Atlantic Ocean:									
	Off Westport, Massachusetts to York Harbor, Maine	3	585	555–620	115	108–124	3	3–3	16.5	16.0–16.8
Aug.	Maryland, Potomac River:									
	Below spawning grounds	4	8	0–19	138	124–150	3	2–3	16.0	14.2–18.4
	Maryland, Chesapeake Bay:									
	Severn Pt. to off Rock Hall	16	97	83–117	148	130–160	3	3–5	18.8	16.5–22.1
	New York, Long Island Sound:									
	Montauk Causeway	1	425	—	134	—	3	—	17.0	—

Table 6—*Continued*

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
Sept.	Maryland, Potomac River: Below spawning grounds	2	18	11-25	178	174-182	—	2-3	16.4	14.5-18.2
	Maryland, Chesapeake Bay: Bay Bridge to off Rock Hall	7	103	84-117	176	164-188	3	3-4	17.1	13.8-20.0
	New York, Long Island Sound: Cedar Beach	1	420	—	155	—	2	—	9.2	—
Oct.	Maryland, Potomac River: Below spawning grounds	5	7	0-17	194	183-217	3	2-4	14.7	12.9-16.2
	Maryland, Chesapeake Bay: Eastern Shore and Bay Bridge	2	102	102-103	203	201-205	—	3-4	18.8	16.5-21.1
1960-61										
Wintering										
Nov.	Maryland, Potomac River: Below spawning grounds	1	45	—	220	—	3	—	14.4	—
	Maryland, Chesapeake Bay: Sharps Is. to Bay Bridge	3	77	48-105	200	192-204	—	2-3-4	15.7	13.6-18.4
Dec.	Maryland, Potomac River: Below spawning grounds	1	8	—	251	—	4	—	19.2	—
	Maryland, Chesapeake Bay: James Is. to Tolchester Beach	3	95	61-122	256	252-261	3	3-4	18.7	17.8-19.5
Jan.	Maryland, Chesapeake Bay: Love Point	1	93	—	286	—	4	—	17.5	—
Feb.	Maryland, Potomac River: Below spawning grounds	1	32	—	309	—	3	—	14.3	—
Mar.	Maryland, Potomac River: Below spawning grounds	13	10	0-29	354	336-374	3	2-4	15.7	13.0-19.2
	Maryland, Chesapeake Bay: Herring Bay	1	111	—	345	—	3	—	14.7	—
	Maryland, Choptank River: Near Secretary	1	97	—	340	—	3	—	17.4	—
1961										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	9	23	5-35	395	366-411	3	3-4	15.9	13.4-22.1
	Below spawning grounds	6	21	3-34	395	389-400	3	2-4	17.7	12.9-22.5
	Maryland, Chesapeake Bay: Off Choptank River and Town Point	2	114	81-140	389	388-390	3	3-3	16.0	15.8-16.2
	Maryland, Nanticoke River: 3 mi. south of Vienna	1	63	—	391	—	3	—	18.6	—
	New York, Atlantic Ocean: Off Jones Beach, Long Island	1	345	—	410	—	3	—	15.9	—
	New York, Long Island Sound: Cedar Beach	1	375	—	400	—	3	—	18.0	—
May	Maryland, Potomac River: Spawning grounds	1	47	—	412	—	3	—	16.9	—
	Maryland, Chesapeake Bay: Off Northeast River	1	157	—	431	—	3	—	14.8	—
	Maryland, Choptank River: Near Windy Hill	1	86	—	403	—	4	—	21.2	—
	New Jersey, Atlantic Ocean: Off Mullica River mouth	1	280	—	406	—	3	—	18.5	—
June	Maryland, Chesapeake Bay: Bloody Pt. and Gum Thicket	2	95	88-101	452	441-463	—	3-4	18.7	18.5-19.0
Feeding										
July	Maryland, Chesapeake Bay: Tilghman Is. to off Rock Hall	3	87	66-98	472	466-484	4	3-4	17.8	16.1-20.2
Aug.	Maryland, Chesapeake Bay: Tangier Bay to off Chester River	5	89	38-117	518	507-524	4	3-5	19.8	17.9-23.8
Oct.	Maryland, Chesapeake Bay: Tilghman Is. and off Rock Hall	2	89	81-98	575	567-582	—	3-4	17.3	16.6-18.0
1961-62										
Wintering										
Nov.	Maryland, Chesapeake Bay: Off Chesapeake Beach	1	105	—	583	—	2	—	12.1	—
Mar.	Maryland, Potomac River: Below spawning grounds	1	19	—	706	—	4	—	20.5	—
	Maryland, Chesapeake Bay: Off Rock Hall	1	117	—	718	—	4	—	17.8	—
1962										
Spawning										
Apr.	Maryland, Potomac River: Below spawning grounds	1	25	—	742	—	3	—	16.8	—
1962-63										
Wintering										
Mar.	Maryland, Potomac River: Below spawning grounds	1	17	—	1,072	—	3	—	16.7	—
1963										
Feeding										
Sept.	Maryland, Chesapeake Bay: Near Havre de Grace	1	138	—	1,259	—	3	—	16.7	—

Table 7. Recaptures by month during the spawning, feeding, and wintering seasons from 631 striped bass tagged and released during the spawning season, April–May 1960, Potomac River, Maryland. [See Table 1 for release data.]

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1960										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	56	12	0–30	12	0–26	3	2–5	16.5	13.4–26.3
	Below spawning grounds	55	8	0–35	9	0–25	3	2–4	16.3	13.2–21.2
May	Maryland, Potomac River:									
	Spawning grounds	31	7	0–18	8	0–50	5	2–17	21.9	11.9–48.0
	Below spawning grounds	7	38	20–50	18	5–29	3	3–8	19.5	13.4–30.5
	Massachusetts, Atlantic Ocean:									
	Nantucket Sound	1	517	—	59	—	3	—	16.0	—
June	Maryland, Potomac River:									
	Spawning grounds	1	46	—	36	—	5	—	20.7	—
	Below spawning grounds	4	47	46–50	40	34–44	3	3–14	22.4	13.7–46.0
	Maryland, Chesapeake Bay:									
	Gooses—Susquehanna Flats	2	134	111–158	48	47–50	—	3–6	21.8	17.2–26.4
Feeding										
July	Maryland, Potomac River:									
	Spawning grounds	2	23	23–23	94	92–97	3	3–3	14.7	13.9–15.5
	Below spawning grounds	1	50	—	32	—	4	—	20.8	—
	Maryland, Chesapeake Bay:									
	Eastern Shore to Swan Point	6	138	126–148	79	66–98	7	3–7	24.7	15.6–28.8
	New York, Atlantic Ocean:									
	Off Montauk Point	1	485	—	76	—	8	—	26.0	—
	Nova Scotia, Bay of Fundy:									
	Off Bear River	1	1,260	—	99	—	3	—	17.8	—
Aug.	Maryland, Potomac River:									
	Below spawning grounds	4	34	26–50	104	96–118	3–4	3–4	17.1	14.3–19.9
	Maryland, Chesapeake Bay:									
	Bay Bridge to Susquehanna Flats	5	143	114–178	119	98–151	4	3–8	23.2	16.4–28.6
Sept.	Maryland, Potomac River:									
	Below spawning grounds	2	42	27–57	141	134–149	—	2–5	16.7	12.7–20.8
	Maryland, Chesapeake Bay:									
	Bay Bridge to Susquehanna Flats	4	160	135–178	133	121–143	7	7–8	32.0	31.2–32.9
	Maryland, Patuxent River:									
	Mouth St. Leonards Cr	1	55	—	153	—	3	—	15.2	—
Oct.	Maryland, Potomac River:									
	Below spawning grounds	2	26	26–26	153	150–156	—	3–5	18.6	14.6–22.6
1960–61										
Wintering										
Nov.	Maryland, Chesapeake Bay:									
	Near Love Point	1	138	—	207	—	3	—	15.6	—
	New York, Atlantic Ocean:									
	Off Montauk Point	1	452	—	201	—	16	—	44.8	—
Dec.	Maryland, Potomac River:									
	Below spawning grounds	1	35	—	221	—	2	—	12.9	—
Jan.	Maryland, Potomac River:									
	Below spawning grounds	2	48	48–48	252	250–254	—	3–7	22.5	17.1–28.0
Feb.	Maryland, Potomac River:									
	Below spawning grounds	1	14	—	321	—	4	—	19.6	—
Mar.	Maryland, Potomac River:									
	Spawning grounds	2	9	5–13	345	327–363	3	3–3	15.1	13.9–16.3
	Below spawning grounds	6	34	22–50	327	317–362	3	3–7	17.2	14.0–26.5
1961										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	18	11	0–21	363	345–391	4	2–7	20.5	12.5–32.5
	Below spawning grounds	4	33	6–57	367	357–388	3–5	3–5	18.5	13.9–22.1
May	Maryland, Potomac River:									
	Spawning grounds	5	2	0–6	362	351–371	3	3–6	21.0	15.1–31.6
	Maryland, Chesapeake Bay:									
	Near James Island	1	100	—	414	—	4	—	21.3	—
Feeding										
Aug.	Maryland, Chesapeake Bay:									
	Off Chester River	1	148	—	514	—	3	—	19.2	—
1962										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	2	14	8–21	731	728–734	—	3–4	17.9	17.8–18.0
Feeding										
July	Maryland, Chesapeake Bay:									
	Off Sparrows Point	1	155	—	822	—	4	—	21.4	—

TABLE 8. Recaptures by month during the wintering, spawning, and feeding seasons from 2,207 striped bass tagged and released during the wintering season, March 1961, Potomac River, Maryland. [See Table 1 for release data.]

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1960–61										
Wintering										
Mar.	Maryland, Potomac River:									
	Spawning grounds	33	18	0–43	15	1–30	3	2–4	15.4	12.0–18.3
	Below spawning grounds	747	5	0–27	6	0–30	3	1–8	15.4	9.8–28.1
	Maryland, Chesapeake Bay:									
	Smith Pt.—mouth Chester River	5	90	55–117	11	6–14	2	2–4	15.6	12.3–21.6
	Maryland, Patuxent River:									
	Sheridan Point	1	53	—	23	—	2	—	14.9	—
	Virginia, Rappahannock River:									
	Near Warsaw	1	90	—	23	—	3	—	16.3	—
	Virginia, Mattaponi River:									
	Clifton Beach	1	82	—	18	—	4	—	22.1	—
1961										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	114	27	3–48	44	27–57	3	2–5	16.0	11.9–23.0
	Below spawning grounds	74	12	0–30	39	25–55	3	2–6	16.5	11.6–26.5
	Maryland, Chesapeake Bay:									
	Tangier Sound—Pooles Is.	10	85	43–110	38	28–54	3	2–3	15.1	13.2–17.3
	Maryland, Choptank River:									
	Dover Bridge—Preston	5	87	75–98	47	33–60	3	2–3	15.9	14.0–17.5
	Maryland, Patuxent River:									
	Magruder Ferry—Holland Cliff	3	78	75–83	44	40–49	3	2–3	15.5	14.4–16.9
	Maryland, Nanticoke River:									
	Vienna—Marshyhope Cr.	2	66	65–67	47	47–48	3	—	16.9	16.6–17.2
	Maryland, Gunpowder River:									
	River mouth	1	135	—	44	—	2	—	14.4	—
	Virginia, Rappahannock River:									
	Urbana—Warsaw	2	90	85–95	48	42–55	3–4	3–4	16.5	15.9–17.2
	Virginia, Piankatank River:									
	Below Freeport	1	76	—	51	—	3	—	17.0	—
May	Maryland, Potomac River:									
	Spawning grounds	44	30	17–50	64	46–82	3	2–5	15.6	12.2–23.5
	Below spawning grounds	8	15	4–30	67	55–77	3	3–5	16.2	13.8–21.0
	Maryland, Chesapeake Bay:									
	Tangier Sound—Turkey Point	8	98	60–150	72	59–88	3	2–5	17.2	11.8–23.1
	Virginia, Rappahannock River:									
	Bowlers Wharf	1	80	—	59	—	3	—	14.6	—
	New York: Atlantic Ocean:									
	Off Amagansett, Long Island	1	428	—	70	—	3	—	15.5	—
	Massachusetts, Weir River:									
	Above Nantasket	1	557	—	85	—	2	—	13.9	—
June	Maryland, Potomac River:									
	Spawning grounds	2	46	38–55	103	100–107	3	—	14.3	13.9–14.7
	Below spawning grounds	7	16	7–23	98	89–108	3	2–4	14.3	11.2–16.1
	Maryland, Chesapeake Bay:									
	Cedar Pt.—Bay Bridge	2	85	61–109	94	82–107	2–3	2–3	14.2	12.8–15.7
	Virginia, Rappahannock River:									
	Near Warsaw	1	103	—	83	—	2	—	11.8	—
	Delaware, Atlantic Ocean:									
	Indian River Inlet	1	255	—	112	—	3	—	15.0	—
	New York, Atlantic Ocean:									
	Off Long Island	2	450	448–453	91	88–94	2–3	2–3	16.6	14.4–18.8
	Connecticut, Atlantic Ocean:									
	Norwalk Harbor	1	462	—	107	—	3	—	17.2	—
	Rhode Island, Atlantic Ocean:									
	Pt. Judith—Narragansett Bay	2	494	484–504	99	82–117	3–5	3–5	21.2	17.2–25.2
	Massachusetts, Massachusetts Bay:									
	Off Greenwood—Quincy Bay	2	575	570–580	97	96–99	3	—	15.8	14.8–16.2
	Massachusetts, Cape Cod:									
	Barnstable Harbor	1	548	—	99	—	3	—	16.0	—
	Massachustets, Narragansett Bay:									
	Off Taunton River	1	546	—	111	—	3	—	16.4	—
	Massachusetts, Nantucket Sound:									
	Area not given	1	528	—	92	—	3	—	16.2	—
	Massachusetts, Merrimack River:									
	Near Amesbury	1	610	—	93	—	3	—	14.8	—
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds	2	12	6–17	137	131–144	3	—	13.7	12.9–14.6
	Maryland, Chesapeake Bay:									
	Tangier Sound—Swan Point	3	100	67–138	130	119–147	3	3–4	14.5	12.6–17.4
	Virginia, Chesapeake Bay:									
	Off Piankatank River	1	64	—	120	—	2	—	12.2	—

TABLE 8—*Continued*

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
	Connecticut, Atlantic Ocean:									
	Off Shippan Point	1	452	—	127	—	3	—	16.9	—
	Rhode Island, Narragansett Bay:									
	Area not given	1	504	—	129	—	3	—	15.9	—
	Nova Scotia, Bay of Fundy:									
	Annapolis Royal Causeway	1	1,240	—	127	—	3	—	16.9	—
Aug.	Maryland, Potomac River:									
	Spawning grounds	1	14	—	159	—	3	—	15.1	—
	Below spawning grounds	5	4	2–4	164	156–167	3	3–4	15.5	13.4–17.5
	Maryland, Chesapeake Bay:									
	Off Solomons—mouth Bush River	11	99	65–118	165	155–175	3	2–5	19.2	12.7–28.5
Sept.	Maryland, Potomac River:									
	Below spawning grounds	2	15	10–20	200	191–210	3–5	3–5	19.6	14.9–24.3
	Maryland, Chesapeake Bay:									
	Eastern Bay—Pooles Island	8	108	88–143	188	180–199	3	3–4	17.3	13.2–22.5
	Virginia, Chesapeake Bay:									
	Off Occohannock Creek	1	78	—	181	—	3	—	13.3	—
Oct.	Maryland, Potomac River:									
	Below spawning grounds	2	31	29–33	231	226–236	2	—	12.8	12.1–13.5
	Maryland, Chesapeake Bay:									
	Above Bay Bridge—Sparrows Point	2	110	110–111	228	221–235	3–4	3–4	15.9	14.3–17.4
	Massachusetts, Massachusetts Bay:									
	Sandwich Beach	1	575	—	224	—	3	—	17.9	—
1961–62										
Wintering										
Nov.	Maryland, Potomac River:.									
	Below spawning grounds	1	17	—	246	—	2	—	12.0	—
	Maryland, Chesapeake Bay:									
	Near Bay Bridge	1	88	—	231	—	3	—	15.8	—
Jan.	Maryland, Chesapeake Bay:									
	Off Kent Shores	1	90	—	313	—	2	—	11.9	—
Mar.	Maryland, Potomac River:									
	Below spawning grounds	10	7	0–21	373	365–387	3	2–4	14.4	12.3–16.4
	Maryland, Chesapeake Bay:									
	Mouth Choptank River—mouth Chester River	2	94	68–121	380	376–385	3–4	3–4	16.8	13.7–20.0
	Maryland, Patuxent River:									
	Near Broome Island	1	83	—	354	—	3	—	16.0	—
	Virginia, Rappahannock River:									
	Near Irvington	1	72	—	368	—	3	—	13.7	—
1962										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	9	28	21–35	398	390–406	3	2–3	14.3	12.6–16.0
	Below spawning grounds	1	8	—	407	—	3	—	14.2	—
	Maryland, Chesapeake Bay:									
	Off Bay Shore	1	75	—	408	—	3	—	14.7	—
May	Maryland, Chesapeake Bay:									
	Gooses	1	71	—	438	—	3	—	15.3	—
	New Jersey, Atlantic Ocean:									
	Off Asbury Park	1	341	—	437	—	3	—	15.8	—
June	Maryland, Potomac River:									
	Below spawning grounds	2	7	7–8	480	475–484	3	—	16.8	14.9–17.7
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds	1	19	—	497	—	3	—	15.6	—
	Maryland, Chesapeake Bay:									
	Love Point—off Rock Hall	2	99	90–108	501	499–503	3–4	3–4	18.3	15.1–21.5
Aug.	Maryland, Chesapeake Bay:									
	Off Rock Hall	1	98	—	528	—	5	—	25.0	—
1963										
Spawning										
Apr.	Maryland, Potomac River:									
	Below spawning grounds	1	0	—	768	—	3	—	14.3	—
Feeding										
July	Rhode Island, Narragansett Bay:									
	Area not given	1	495	—	849	—	3	—	16.0	—
Oct.	Maryland, Chesapeake Bay:									
	Tangier Sound	1	46	—	971	—	3	—	18.3	—
1964										
Feeding										
Aug.	Maryland, Chesapeake Bay:									
	Bay Bridge	1	105	—	1,261	—	3	—	16.0	—

TABLE 9. Recaptures by month during the spawning, feeding, and wintering seasons from 474 striped bass tagged and released during the spawning season, April–May 1961, Potomac River, Maryland. [See Table 1 for release data.]

Recapture data							Tagging data			
Year Season Month	Locality	No. recaptures	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Predominate	Range	Mean	Range
1961										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	88	4	0–16	2	0–5	3	2–8	17.1	12.5–30.0
	Below spawning grounds	3	26	26–27	2	0–2	3	3–4	17.9	14.4–23.0
May	Maryland, Potomac River:									
	Spawning grounds	17	3	0–16	12	5–19	3	3–5	17.8	13.5–23.1
	Below spawning grounds	6	37	33–43	6	5–11	3	3–6	17.4	14.2–29.0
June	Maryland, Potomac River:									
	Spawning grounds	1	7	—	47	—	3	—	12.9	—
	Below spawning grounds	1	50	—	41	—	5	—	22.6	—
	Maryland, Chesapeake Bay:									
	Poplar Island	1	123	—	60	—	3	—	12.9	—
Feeding										
July	Maryland, Potomac River:									
	Below spawning grounds	1	20	—	71	—	3	—	16.6	—
	Maryland, Chesapeake Bay:									
	Swan Point	1	134	—	68	—	4	—	22.0	—
Aug.	Maryland, Chesapeake Bay:									
	Love Point—off Rock Hall	7	132	110–144	117	106–128	5	3–7	23.8	14.7–31.3
Sept.	Maryland, Potomac River:									
	Below spawning grounds	1	68	—	142	—	3	—	14.4	—
	Maryland, Chesapeake Bay:									
	Bay Bridge—mouth Chester River	4	122	118–126	137	131–140	3	3–5	19.6	13.5–25.4
	Virginia, Chesapeake Bay:									
	Off Piankatank River	1	96	—	151	—	3	—	14.7	—
Oct.	Maryland, Potomac River:									
	Below spawning grounds	2	34	26–43	178	163–184	—	3–4	18.7	15.5–22.0
	Maryland, Chesapeake Bay:									
	Herring Bay—Bay Bridge	2	128	120–136	176	173–179	—	3–4	18.4	13.7–23.1
	Maryland, Patuxent River:									
	Mouth Cat Creek, St. Marys County	1	108	—	164	—	3	—	12.6	—
1961–62										
Wintering										
Dec.	Maryland, Potomac River:									
	Below spawning grounds	1	50	—	227	—	4	—	21.5	—
Feb.	Maryland, Chesapeake Bay:									
	Mouth Little Choptank River	1	93	—	304	—	3	—	13.2	—
Mar.	Maryland, Potomac River:									
	Spawning grounds	1	35	—	340	—	2	—	12.4	—
	Below spawning grounds	7	32	31–36	328	315–338	3	3–4	16.4	13.7–20.5
	Maryland, Chesapeake Bay:									
	Off Rock Hall	1	144	—	325	—	3	—	14.1	—
1962										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	9	3	0–13	344	337–353	3–4–5	3–4–5	19.2	13.8–23.3
	Below spawning grounds	1	26	—	353	—	6	—	29.2	—
	Maryland, Chesapeake Bay:									
	Sharps Island—off Aberdeen Proving Grounds	2	134	108–160	358	353–364	3	—	15.6	15.1–16.2
June	Maryland, Chesapeake Bay:									
	S. Chesapeake Beach	1	112	—	427	—	3	—	15.8	—
Feeding										
Oct.	Maryland, Potomac River:									
	Below spawning grounds	1	55	—	539	—	3	—	13.5	—
	Maryland, Chesapeake Bay:									
	Near Kent Point	1	108	—	530	—	4	—	21.6	—
1962–63										
Wintering										
Mar.	Maryland, Potomac River:									
	Below spawning grounds	1	43	—	700	—	3	—	13.1	—
1963										
Spawning										
Apr.	Maryland, Potomac River:									
	Spawning grounds	1	6	—	718	—	3	—	13.7	—
	Below spawning grounds	1	23	—	711	—	4	—	18.8	—

one striped bass tagged in the York River in February was caught in the Potomac River the following month. Mansueti (1961: 17–36) stated that several striped bass tagged during the wintering season in the Maryland part of Chesapeake Bay were caught in the Potomac during the following spawning season.

TABLE 10. Recaptures by season from 6,197 striped bass tagged and released during the wintering season, 1,854 tagged and released during the spawning season, and 922 tagged and released during the feeding season, Potomac River, Maryland, 1959–61.

Season tagged and released	Season of recapture	Area of recapture							
		Maryland				Virginia			
		Potomac River		Chesapeake Bay		Chesapeake Bay		Outside Chesapeake Bay	Total
		Spawning grounds	Below spawning grounds	Tributaries other than Potomac	Bay proper	Tributaries	Bay proper		
Wintering season	Season of release	90	1,082	1	9	2	2	1	1,187
	Following spawning	451	594	20	47	6	2	25	1,145
	Following feeding	3	42	—	67	—	2	10	124
	2nd wintering	1	41	2	12	1	1	—	58
	2nd spawning	32	21	2	8	—	—	5	68
	2nd feeding	—	1	—	14	—	—	1	16
	3rd wintering	—	4	—	2	—	—	—	6
	3rd spawning	1	4	—	—	—	—	—	5
	3rd feeding	—	1	—	4	—	—	1	6
	4th wintering	—	1	—	—	—	—	—	1
	4th feeding	—	—	—	2	—	—	—	2
	Subtotal	578	1,791	25	165	9	7	43	2,618
Spawning season	Season of release	230	108	—	4	—	—	2	344
	Following feeding	4	22	2	43	—	1	3	75
	Following wintering	6	28	—	4	—	—	—	39
	2nd spawning	50	9	1	6	—	—	1	77
	2nd feeding	—	3	—	3	—	—	—	6
	2nd wintering	—	4	—	2	—	—	—	6
	3rd spawning	4	2	—	—	—	—	—	6
	3rd feeding	—	—	—	1	—	—	—	1
	4th spawning	—	—	—	1	—	—	—	1
	Subtotal	294	186	3	64	—	1	7	555
Feeding season	Season of release	—	25	—	—	—	—	—	25
	Following wintering	3	92	—	—	—	—	—	95
	Following spawning	7	21	—	4	—	—	2	34
	2nd feeding	—	8	—	2	—	—	—	10
	2nd wintering	—	3	—	—	—	—	—	3
	2nd spawning	—	1	—	—	—	—	—	1
	3rd feeding	—	—	—	1	—	—	—	1
	3rd wintering	—	1	—	—	—	—	—	1
	4th feeding	—	2	—	—	—	—	—	2
	Subtotal	10	153	—	7	—	—	2	172
	Total	882	2,130	28	236	9	8	52	3,345

MOVEMENT OUT OF CHESAPEAKE BAY

About 0.6% of the striped bass tagged in the Potomac River moved out of Chesapeake Bay and northward along the Atlantic coast as far as the Bay of Fundy. Vladykov and Wallace (1952: 174) reported that 2 fish of 662 striped bass they marked during October 1937 in the Potomac migrated out of the bay.

Most of the tagged fish recaptured outside Chesapeake Bay left the river in early spring. Forty-three of the outside recaptures were from fish tagged during the wintering season, and 68% of these were recaptured in the following spawning season. One striped bass tagged in the winter was recaptured outside the bay within 8 days, 275 miles from the point of release; 25 fish in the following spawning season were caught 20 to 117 days after release, and

190 to 668 miles from the point of release; 10, in the following feeding season were recovered from 108 to 224 days after release, and from 420 to 1,270 miles from the release point; and 7 at liberty more than 1 year were retaken at various distances from the point of release (Fig. 4). Two tagged striped bass from the spawning season tagging were recaptured outside Chesapeake Bay within the season of release, and three were recovered outside the bay in the following feeding season (Fig. 5). Of these five fish, three were 8 to 10 years old and most likely had spawned before leaving the river. Two fish tagged during the feeding season were recaptured outside the bay, 186 and 200 days after release and 565 and 750 miles from the release point (Fig. 6). Both of these fish were 2 years old at release; they probably left the river the following spring at which time they would have been 3 years old.

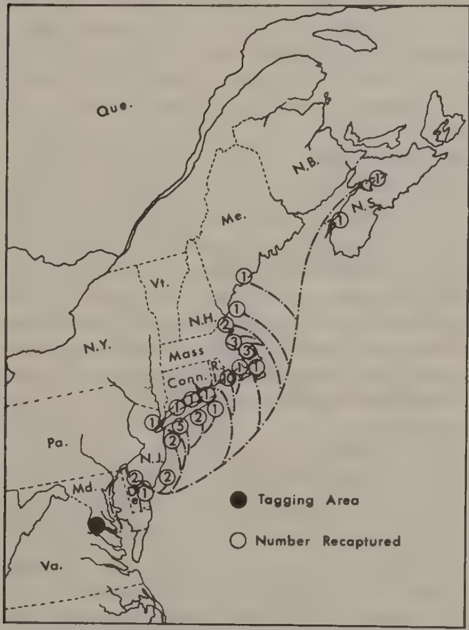

Fig. 4. Recaptures outside Chesapeake Bay from striped bass tagged and released during the wintering seasons, Potomac River, Maryland, 1959–61.

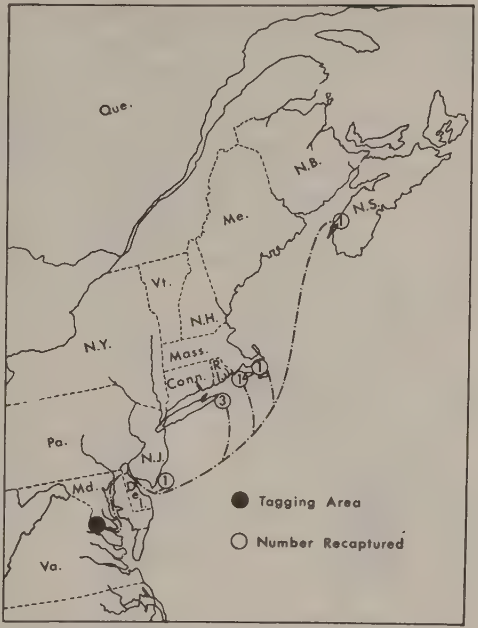

Fig. 5. Recaptures outside Chesapeake Bay from striped bass tagged and released during the spawning seasons, Potomac River, Maryland, 1959–61.

Most of the "outside" recaptures were 3 years old when they left the river. About 88% of the fish tagged during the wintering season and recaptured outside the bay in the following spawning and feeding seasons were 3 years old. Merriman (1941: 33–46) found that about 90% of the striped bass examined for sex off Long Island and New England coasts were immature females, 2 or 3 years old. Because of the difference in the age at maturity of the males and females (males spawn for the first time at the end of their second year and females not before the end of their fourth year), many of the 2- and 3-year-old males do not take part in the spring migrations but stay behind to spawn with the larger and older females. We found no evidence that Potomac River striped bass younger than 2 years undertake coastal migrations.

We found some evidence that tagged striped bass migrated outside Chesapeake Bay to the ocean through the Chesapeake and Delaware Canal. One tagged fish from the winter tagging was recaptured in Dela-

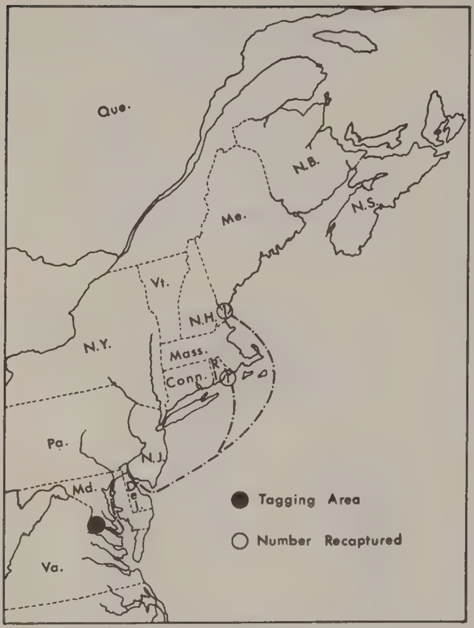

Fig. 6. Recaptures outside Chesapeake Bay from striped bass tagged and released during the feeding season, Potomac River, Maryland, 1959.

ware Bay near the canal entrance 20 days and 190 miles from the date and point of release. Another tagged fish was taken near the Delaware River mouth 40 days and 153 miles from the date and point of release. No fish were recaptured south of the James River bridge in the Virginia part of Chesapeake Bay or south of Indian River Inlet off the Delaware coast. If tagged fish had moved out through the mouth of the bay, most likely some would have been recaptured in the Atlantic Ocean off the Virginia coast.

Recaptures of tagged striped bass on their coastal migration indicated that they moved northward along the coast in early spring. Tagged fish were recaptured during the spawning season throughout the coastal area from Delaware to Maine. In the summer the tagged fish were scattered along the New England coast. During the feeding season they were recaptured from Long Island to Nova Scotia. Some fish presumably moved southward in fall and reached wintering grounds in Chesapeake Bay and its tributaries by October and November. Recaptures of some tagged fish along the New England coast in the early spring one year after release, suggested that some coastal migrants wintered over and spent the following spring and summer along the coast before returning to Maryland waters. Merriman (1941: 33–46) found similar movement by striped bass tagged and released in Connecticut and Long Island waters, i.e., a coastal northward migration in the spring, no movement of any consequence in the summer, and a southward migration in fall and early winter.

Distances Traveled and Days at Large

Although striped bass were tagged at several localities throughout the Potomac River in different seasons, most of the recoveries were made in the vicinity of the release site regardless of the time at large. Of the 3,345 recaptures, about 69% were made less than 25 miles from the release site and within 25 days after release. Distances traveled and days at large by the tagged fish that were recaptured more than 25 miles from the release site varied greatly (Table 11). For example, one 3-year-old striped bass was recaptured that was tagged during the wintering season and had been at large 763 days, yet was recaptured during the spawning season less than 1 mile from the release site. At the other extreme, one 3-year-old striped bass that had been tagged during the spawning season and had been at large 99 days, was recaptured during the feeding season approximately 1,260 miles from the release site.

Of the 273 tagged fish recovered after the first year, 253 were recaptured more than one year after release, 15 in the third year, 4 in the fourth year, and 1 in the fifth year. The last mentioned fish was released during the 1959 wintering season and was recaptured during the feeding season near Chesapeake Bay Bridge 1,621 days after release. The fish weighed 7 lbs. and 12 oz. and was 24.6 inches long at the time it was tagged, but its weight and length at recapture are unknown. To our knowl-

Table 11. Summary of days at large and distance from tagging site of recaptured striped bass from 8,973 fish tagged and released during the wintering, spawning, and feeding seasons, Potomac River Maryland, 1959–61.

Season	Fish tagged	Fish recaptured												
		Days at large	Season			Total		Distance from release site in miles	Season			Total		
			Wintering	Spawning	Feeding	No.	%		Wintering	Spawning	Feeding	No.	%
Wintering	6,197	Less than 30	1,049	306	—	1,355	51.7	Less than 25	1,048	633	43	1,724	65.9
		30–90	145	709	—	854	32.6	25–50	173	475	7	655	25.0
		91–180	10	119	88	217	8.3	51–100	19	48	36	103	3.9
		181–300	4	6	37	47	1.8	101–200	11	38	23	72	2.8
		301–500	43	68	5	116	4.4	201–500	1	10	32	43	1.6
		501–1,000	6	5	14	25	1.0	501–1,000	—	14	5	19	0.7
		More than 1,000	1	—	3	4	0.2	More than 1,000	—	—	2	2	0.1
		Subtotal	1,258	1,213	147	2,618	42.2	Subtotal	1,252	1,218	148	2,618	42.2
Spawning	1,854	Less than 30	—	316	—	316	56.9	Less than 25	14	308	12	334	60.2
		30–90	—	28	14	42	7.6	25–50	25	97	18	140	25.2
		91–180	9	—	61	70	12.6	51–100	4	5	9	18	3.3
		181–300	2	—	—	2	0.4	101–200	3	11	41	55	9.9
		301–500	28	77	1	106	19.1	201–500	—	—	4	4	0.7
		501–1,000	6	6	6	18	3.2	501–1,000	—	2	1	3	0.5
		More than 1,000	—	1	—	1	0.2	More than 1,000	—	—	1	1	0.2
		Subtotal	45	428	82	555	29.9	Subtotal	46	423	86	555	29.9
Feeding	922	Less than 30	51	—	25	76	44.2	Less than 25	96	24	35	155	90.1
		30–90	33	—	—	33	19.2	25–50	3	5	—	8	4.6
		91–180	11	34	—	45	26.2	50–100	—	3	2	5	2.9
		181–300	—	—	5	5	2.9	101–200	—	1	1	2	1.2
		301–500	3	—	5	8	4.6	201–500	—	—	—	—	—
		501–1,000	1	1	3	5	2.9	501–1,000	—	2	—	2	1.2
		More than 1,000	—	—	—	0	0.0	More than 1,000	—	—	—	0	0.0
		Subtotal	99	35	38	172	18.6	Subtotal	99	35	38	172	18.6
Total	8,973		1,402	1,676	267	3,345	37.3		1,397	1,676	272	3,345	37.3

edge, this is the longest time at large for a tagged striped bass.

Vladykov and Wallace (1952: 171) reported from their recaptures of striped bass tagged in the Potomac River that the river stocks appeared to be almost stationary. Our recaptures, however, show that a number of tagged fish moved out of the river and traveled great distances within Chesapeake Bay and several made greater migrations outside the bay. Of the fish we tagged in the Potomac and recaptured outside the river of release, 281 were caught in Chesapeake Bay and tributaries other than the Potomac from 38 to 200 miles from the point of release (average distance, 102 miles). For the 52 recaptures outside Chesapeake Bay, the distances traveled ranged from 190 to 1,270 miles and averaged 515 miles. Three of the recaptures were made in the Bay of Fundy, Nova Scotia, more than 1,200 miles from the release site.

The rate at which striped bass may travel is shown by the recapture of several tagged fish. Four tagged fish that were recaptured 78 to 1,260 miles from the point of release in 3 to 99 days after tagging had traveled an average of 15 miles per day. It appears that the farther away from the release point the recapture was made, the fewer miles per day the fish traveled. One tagged fish recaptured off the New Jersey coast traveled at least 34 miles per day; another recaptured off the New York coast traveled at least 20 miles per day; and one recaptured in the Bay of Fundy traveled at least 13 miles per day. The distances were measured in a straight line through Chesapeake and Delaware Bays and along the coast; probably the fish averaged more miles per day than the data indicate.

Relation Between Length of the Tagged Fish and Distances Traveled

Mansueti (1958: 22 and 1961: 31) reported that the larger of the striped bass tagged in the Maryland part of Chesapeake Bay traveled somewhat longer distances than smaller individuals. Fish at 16 inches fork length and above traveled about 11 miles more, on the average, than did those below this length. He pointed out, however, that his results probably were affected by differences in fishing intensity among recapture areas, in seasonal fishing patterns, and in gears catching the tagged fish. We could not demonstrate a definite relation between length or age of the tagged fish and distances traveled. Some fish at all ages from 2 to 5 years (14 to 20 inches long) traveled equally long distances. Merriman (1941: 33–45) found little evidence that striped bass younger than 2 years old traveled great distances.

Mansueti (1961: 33) estimated that male striped bass 16 inches long or longer traveled over 5 miles per day more than those below this length, and females and fish of unknown sex 16 inches and above traveled over 15 miles per day farther on the average. Because of the small number of recaptured fish of known sex, we were unable to determine any relation between sex and distances traveled by the tagged fish.

HOMING TENDENCY OF STRIPED BASS

The possibility that spawning striped bass may return to the same spawning area each year was suggested by the recapture years later of fish tagged on the same spawning grounds during a previous spawning season (Table 12). Of the 37 fish recaptured during the spawning season one year after tagging the previous spawning season, 32 were taken in the Potomac River (25 in the spawning area and 7 below the spawning area), 3 were caught in the Maryland part of Chesapeake Bay, and 1 was taken outside Chesapeake Bay off the New Jersey coast. Of the 32 fish recaptured in the Potomac one year after release on a spawning area, 22 were males, 1 was a female, and 9 were of undetermined sex. Four tagged fish of undetermined sex were recaptured in the Potomac two years after release, 2 in the spawning area and 2 below the spawning area. Hollis (1960: 19), Hollis and Davis (1955: 2), and Mansueti (1961: 24) also suggested from tag returns that striped bass return to the same spawning area in successive years.

Implications for Management

Elements of the Potomac River striped bass stock are present in the river throughout the year and long-range movements are made by a small number of the fish. Preliminary results of studies by Mansueti (1961: 33), Hollis and Davis (1955: 2), and Massmann, Pacheco, and Richards (1959: 44) suggested that long-range movements are carried out by small numbers of striped bass from stocks throughout Chesapeake Bay and its tributaries. In our study the recapture of tagged fish in close proximity to the release site indicated that few fish left the river during the spawning season, and that fish that spawned in the Potomac would return to spawn in successive years. One- and 2-year-old fish that spent the feeding season in the river, remained in the river during the wintering season also. On the basis of the above findings we concluded that the Potomac River striped bass fishery can be managed as an individual stock.

Merriman (1941: 30–31), Vladykov and Wallace (1952: 174–177), and Mansueti (1961: 33) concluded that the migratory stock along the Atlantic coast was produced in Chesapeake Bay but that it was a relatively small portion of the Chesapeake Bay population. The 52 fish from the Potomac River (0.6% of the fish tagged) recovered outside the bay could represent a significant contribution by this river to the outside fisheries. It is reasonable to infer, however, that the percentage of the population that migrates from the bay is extremely small.

Parts of several striped bass stocks spend the wintering season in the Potomac River. Recaptures of fish tagged in the river during the wintering season were made within the season of release and the following spawning season throughout Chesapeake Bay and the Rappahannock and York Rivers in Virginia and the Little Choptank, Choptank, Nanticoke, Patuxent, Chester, Blackwater, and Gunpowder

TABLE 12. Recaptures during the spawning season one and more years later of striped bass tagged on the spawning grounds in the Potomac River, Maryland, in April and May 1959–61.

Recapture data							Tagging data			
Years after release	Locality	Number	Distance from tagging site in miles		Days at large		Age		Fork length in inches	
			Mean	Range	Mean	Range	Pre dom- inate	Range	Mean	Range
1	Maryland, Potomac River:									
	Spawning grounds	25	5	0–16	357	339–375	2–3–4	1–5	18.3	11.1–26.3
	Below spawning grounds	7	26	6–43	354	330–373	2–4	1–6	17.4	11.1–29.2
	Maryland, Chesapeake Bay:									
	James Island—off Aberdeen Proving Grounds	3	126	103–168	378	354–414	3	—	16.9	15.1–19.3
	Maryland, Patuxent River:									
	Near Benedict Bridge	1	148	—	350	—	2	—	15.2	—
	New Jersey, Atlantic Ocean	1	365	—	355	—	2	—	15.5	—
2	Maryland, Potomac River:									
	Spawning grounds	2	3	0–6	716	712–719	2–3	2–3	15.6	13.7–17.8
	Below spawning grounds	2	27	23–31	724	710–738	4–5	4–5	22.7	18.8–26.6
3	Maryland, Chesapeake Bay:									
	Gooses Area	1	111	—	1,145	—	5	—	27.8	—

Rivers in Maryland. Undoubtedly, some Potomac River striped bass spend the wintering season in the bay and other tributaries, but no definite pattern of overwintering could be demonstrated.

Summary and Conclusions

During the wintering, spawning, and feeding seasons of 1959–61, 8,973 striped bass were tagged and released in the Potomac River, Maryland. Of the 3,345 recaptures of tagged fish, 3,276 (98.0%) were in the Maryland part of Chesapeake Bay and tributaries; 17 (0.5%) in the Virginia part of Chesapeake Bay and tributaries; and 52 (1.5%) outside Chesapeake Bay along the Atlantic coast from Delaware to Nova Scotia.

Tagged fish showed the following seasonal movement. (1) Wintering season (November–March): The tagged fish were active and some individuals traveled several miles a day. Shortly after release, several tagged fish moved outside the Potomac. In the latter part of the wintering season and early part of the following spawning season, many of the tagged fish moved from the lower river upstream to the spawning grounds. (2) Spawning season (April–June): The bulk of the tagged fish moved into the spawning area early in the season and remained there for most of the spawning period. Most of the tagged fish moved downstream in the latter part of the spawning season and congregated in the lower river; several moved into Chesapeake Bay and tributaries, and a few left the bay. (3) Feeding season (July–October): Tagged fish were scattered throughout Chesapeake Bay and tributaries and the lower Potomac. Most of the fish tagged in the Potomac during the feeding season remained in the river during the season of release and the following wintering season; a few were scattered throughout the Maryland part of Chesapeake Bay and tributaries other than the Potomac.

Significant findings were: (1) Some striped bass which overwintered in the Potomac River were recaptured during the following spawning season in the York and Rappahannock Rivers in Virginia, and the Choptank, Nanticoke, Patuxent, Chester, Blackwater, and Gunpowder Rivers in Maryland; (2) a few of the Potomac River striped bass stock moved outside Chesapeake Bay in early spring and spent the summer and autumn along the northeast Atlantic coast; and (3) spawning striped bass returned to the same spawning area in successive years.

We concluded that (1) the Potomac River is a significant contributor to the striped bass stocks along the northeast Atlantic coast; and (2) the Potomac River striped bass fishery can be managed as an individual stock.

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DISTRIBUTION AND MIGRATION OF ALBACORE (*THUNNUS ALALUNGA*) IN THE PACIFIC OCEAN*

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ABSTRACT

Albacore (*Thunnus alalunga*) are widely distributed in the Pacific Ocean. In temperate waters of the North Pacific they are found near the surface and are the basis of the troll and live-bait fishery off the west coast of North America, and the live-bait fishery of Japan. Albacore are also found in deeper water in temperate, subtropical, and tropical areas, where they support the vast longline fisheries of the North and South Pacific.

A composite size frequency distribution of albacore sampled from the U.S. west coast fishery in 1949-58 showed a length range of 44 to 101 cm, with a dominant mode at 65 cm and a lesser mode at 76 cm. The length range of albacore caught in the Japanese live-bait fishery usually is from about 62 to 97 cm with a dominant mode at 83 cm. The range in length of albacore caught by the Japanese longline fishery in the North Pacific is about 50 to 120 cm. Longline fishery in the South Pacific takes albacore ranging from 67 to 111 cm.

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Albacore of the North Pacific spawn in tropical and subtropical waters; the young migrate to temperate waters in their second year, and appear in the catches of the American fishery in large numbers in their third year. The fish then spend several years in temperate waters. The younger fish (2-4 years old) tend to linger in the eastern Pacific for the first few years; progressively more fish move into the western Pacific as they grow older. Albacore attain sexual maturity in their sixth year. The mature fish return eventually to subtropical and tropical waters to spawn.

INTRODUCTION

Albacore (*Thunnus alalunga*) are widely caught throughout the Pacific. Some fisheries concentrate on the surface-swimming segment of the population, others on the deep-swimming. The fish are known to engage in transpacific migrations in the North Pacific, but whether they do so in the South Pacific is unknown. This paper reviews the state of our knowledge of the distribution and migration of the species in the Pacific.

DISTRIBUTION OF ALBACORE

Much of our knowledge of the distribution of albacore, both at the surface and beneath it, is based upon the results of commercial fishing. Thus what is known about the distribution of the fish may be largely a function of the range of commercial fishing vessels.

Surface-swimming albacore

There are two major surface fisheries for the albacore in the North Pacific--the North American and the Japanese. Off the west coast of North America, albacore occur off Mexico near the Revillagigedo Islands and northward along the coast into the Gulf of Alaska (Clemens and Craig, 1965). Most catches are made between central Baja California and the Columbia River. The fish are taken only a few hundred miles to sea. Off the Japanese Islands, the surface fishery extends farther seaward, but is relatively narrow, covering 11 degrees of latitude (lat. 27° to 38° N) rather than the 20 degrees of the eastern shore of the Pacific (Fig. 1). Both surface fisheries are in temperate waters.

Both fisheries for albacore are highly seasonal. The fish appear off the North American coast in May or June, remain through the summer and fall, and disappear in December. The center of abundance is off Baja California early in the summer and shifts northward as the season progresses. In Japan albacore typically first appear in April south of Honshu, the main island. As the season progresses, the center of abundance shifts northeasterly, describing a gentle arc, so that in July, near the end of the season, fishing is centered well offshore between long. 150° and 160° E and lat. 30° and 35° N.

From 1951 to 1956 the Japanese albacore fishing grounds were extended eastward, from about long. 155° to 165° E, thereby extending the known range of surface-swimming albacore. This expansion of the fishery reflected the greater number of larger vessels in the fleet that were capable of operating far offshore (Van Campen, 1960).

Surface-swimming albacore have been sporadically captured by research vessels in the North Pacific between about long. 170° E and 135° W, and lat. 30° and 45° N (Shomura and Otsu, 1956; Graham, 1957).

Less is known about the distribution of surface-swimming albacore in the South Pacific. They occur off southeastern Australia, from southernmost Tasmania to near Montague Island in New South Wales, from October to June (Serventy, 1941). Chile has a small coastal troll fishery that also is conducted during the Southern Hemisphere summer (de Buen, 1958).

Deep-swimming albacore

Albacore are widely distributed at cool subsurface levels in the Pacific Ocean (Fig. 2). In the North Pacific they are caught from the coast of Japan to about long. 125° W, only a few hundred miles off the western coast of North America. In a north-south direction, subsurface albacore are caught from about lat. 45° N to the Equator, at least in the western North Pacific. The void on the eastern side of the North Pacific may merely reflect a lack of fishing.

In the South Pacific, albacore form the basis of a longline fishery that extends from the east coast of Australia to about long. 85° W in the eastern end of the fishery and from the Equator to about lat. 45° S in the western end.

In the North Pacific, albacore are found throughout the year in the general area of the longline fishery. Their abundance shows a marked seasonality, however. The longline fishery begins to be of consequence in October, when the fish are most abundant between long. 170° E and 170° W and lat. 40° and 30° N. As the season progresses the center of abundance shifts westward and slightly southward; by the end of the season, in the spring, it is between long. 140° and 160° E and lat. 35° and 25° N.

The distribution of albacore in the South Pacific also changes seasonally. From January through April most fishing is confined to the area between the Equator and lat. 20° S; the best catches are made between lat. 10° and 20° S. In June the fishing grounds expand southward to about lat. 25° to 40° S; catches are relatively good between lat. 10° and 30° S (in certain areas even as far north as the Equator). From July through September catches are relatively good from about lat. 5° to 30° S, and are best between lat. 20° and 30° S. In October and November, catches are relatively good in a wide area from about lat. 10° to 30° S. In December fishing again is confined mostly to the north of about lat. 25° S; the best catches are between lat. 10° and 20° S. Thus fishing is done throughout the year in the area north of about lat. 25° S, but is restricted to the southern winter and spring in the area south of lat. 25° S.

Environmental factors affecting distribution

Although the relation between the distribution of albacore and the environment is not yet well understood, it may be useful to examine the distribution of the fish in relation to some broad features of their environment.

Superimposed over the distributional charts (Figs. 1 and 2) are selected surface isotherms (from U.S. Navy Hydrographic Office, 1944). One noticeable general feature is that albacore are most abundant in areas where the surface water is warmer than about 15.6° C (60° F). Temperature is believed to play an important role in the distribution of albacore (this subject is discussed later).

The fisheries appear to be related to the major current systems of the Pacific Ocean (Fig. 3). The Japanese winter longline and spring-summer pole-and-line fisheries for albacore are in the North Pacific Current, the Kuroshio, and the Kuroshio Extension Current. The U.S. west coast albacore fishery is in the cool waters of the California Current. In the South Pacific, the only major fishery for albacore, the longline fishery, is in waters generally under the influence of the South Equatorial Current.

Japanese scientists believe that the development of the surface albacore fishery each year is influenced by the manner in which the seasonal warming of the fishing area by the Kuroshio Current progresses. In some years the Kuroshio pushes northward in such a way that pockets of cool water lie close to shore. This phenomenon is thought to concentrate albacore schools and to favor good fishing. In other years, the Kuroshio may develop unusually early, so that these pockets of cool water either do not develop or are short-lived. Then the schools move offshore to the northeastward more rapidly and fishing close to shore is poor (Van Campen, 1960). Changes in water temperature are assumed to be the underlying cause of this behavior. Among various Japanese authors who have discussed the influence of temperature on albacore catches, Kawasaki and Asano (1962) presented data showing that most albacore are caught in waters with surface temperatures between 21° and 23° C (Fig. 4).

During the 1957, 1958 and 1961 seasons in the U.S. west coast albacore fishery, albacore were most plentiful in waters ranging from 62° (16.7° C) through 67° F (19.4° C) (Clemens and Craig, 1965). If the run was composed predominantly of large fish (>20 pounds or 9.1 kg) fishing was best in warmer (>67° F or 19.4° C) parts of the preferred temperature range. If the run consisted of predominantly small fish, fishing was good in somewhat cooler water.

Suda and Shiohama (1962) found a somewhat similar pattern in the Japanese winter longline fishery. Different length groups of albacore were found in waters of different surface-temperature ranges; the larger fish were in a wider temperature range (Fig. 5).

In the western South Pacific, Yamanaka (1956) noted a discontinuity in the oceanic structure, extending east-west and centered at about lat. 10° S, that was conspicuous during November and February but was not pronounced during

June and July. When the discontinuity was conspicuous, good albacore fishing was restricted to the south of it, but when the discontinuity was not clear, good fishing could be found both north and south of lat. 10° S. He concluded that the discontinuity acted as a limiting factor in the distribution of albacore in the southern summer.

MIGRATION

The ocean-wide migration of albacore in the North Pacific Ocean was described by Clemens (1961, 1962, 1963) and Otsu and Uchida (1962, 1963). The patterns of migration proposed by these writers are in good general agreement. The extensive movements were described as size (and age) specific. Therefore, a description of the migration of the North Pacific albacore must consider the size composition of albacore taken in the various localities.

Sizes and estimated ages of exploited fish

A composite length-frequency distribution for each of the North Pacific fisheries is shown in Fig. 6. The modal lengths of the age groups are approximations based on the appearance of the modes as well as on an albacore growth curve derived from tag recovery data (Otsu, 1960). The absolute ages have been estimated on the assumption that the 30-35 cm fish which occasionally enter the commercial catches are 1 year old and therefore that the albacore are 2 years old when (at a length of 50 cm) they first enter the fisheries in significant numbers. Clemens (1961), on the other hand, has postulated that the fish are 1 year old at a size of around 50 cm. Aside from this disagreement in the assignment of absolute ages, the growth curves described by the two authors are not significantly different.

The American fishery generally exploits three groups of fish, which are approximately 2, 3 and 4 years old (55, 65 and 76 cm). The 3-year-olds are usually the most abundant. A few fish older than 4 years also appear in the catches. The Japanese winter longline fishery is based on a wide range of ages, from 2 to 9 years, and perhaps older. Most abundant are the 4- and 5-year-old fish with modal sizes at 79 and 88 cm. The Japanese live-bait fishery generally exploits three age groups, 4-, 5-, and 6-year olds, whose modal lengths are about 75, 83 and 93 cm. The 5-year-olds are usually most abundant. One-year-old albacore occur infrequently.

Migration of albacore within and between fisheries

The migration of albacore within the areas of the established fisheries is reflected by the movements of the fishery. The American fishery moves northward along the coast as the season progresses, that is, from May or June through September and October or even later in the year. The Japanese winter longline fishery shifts southwestward from about October to March, and the Japanese live-bait fishery develops off Southern Japan in April or May, gradually moves north and northeast, and ends about July near 160° E.

It is postulated that albacore undertake no more than one transpacific crossing during a single year, on the basis of (1) information on the distribution of fish in areas outside of these fisheries during various times of the year, collected during exploratory fishing cruises by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu (Shomura and Otsu, 1956; Graham, 1957), and (2) interpretation of tagging results (Otsu and Uchida, 1963). The movements between established fisheries appear to be rapid, those within the areas of the fisheries slow.

Model of migration

Fig. 7 represents diagrammatically the movements of albacore among the three fisheries in the North Pacific on the basis of size (age) groups. The same concept is depicted in another way in Fig. 8, which shows the migratory pattern of each age group. Briefly, the pattern is as follows: Spawning takes place during the early summer in a broad band of subtropical waters extending westward from the Hawaiian Islands (about lat. 10°-20° N). After hatching, the larvae drift with the North Equatorial Current. During most of the first year they remain in subtropical waters. When they reach a length of about 30 cm, they migrate north into temperate waters, i.e., into the areas of the three fisheries, but do not immediately join the exploited stock. They begin to enter the commercial catches in numbers when they reach the age of 2 (about 50 cm) and only at age 3 is recruitment completed.

The near absence of 2-year-olds in the Japanese live-bait fishery and the relatively small number of fish of this age group in the longline fishery suggest that recruitment into the exploited stock occurs primarily in the American fishery. Although 1-year-old fish are occasionally taken in the Japanese live-bait fishery, it appears that the largest concentrations of the younger fish (1 to 3 years old) are in the eastern Pacific.

In general, the model indicates a greater volume of migration of the commercial sizes of albacore westward, from the American into the Japanese fishery, than vice versa. A significant portion of the fish entering the American fishery at ages 2 and 3 does not migrate directly into the Japanese fisheries, but instead is exploited over three or four seasons in the American fishery. As the fish grow older, westerly migration increases. Few fish move from the Japanese fisheries into the American fishery.

Migration of albacore in the South Pacific Ocean

No information is now available on the migration of the South Pacific albacore. From knowledge of the migration of the North Pacific albacore, however, it may be postulated that the juvenile component of the South Pacific population migrates between the coastal waters of Australia and Chile.

The albacore off Chile are reportedly of lengths similar to those in the Japanese live-bait fishery in the North Pacific, and the length of the fish off Australia resembles that of fish taken in the American fishery. It is possible that volume of movement in an easterly direction is greater in the South Pacific than in the North Pacific. As the fish mature in temperate waters, they move north into subtropical and tropical waters in areas north of lat. 30° S, where they form the adult, reproductive segment of the population. It is this segment that presently supports the extensive South Pacific longline fishery.

Within this area of the longline fishery, between the Equator and about lat. 30° S, the size of fish gradually increases from the Equator southward to about lat. 20°-25° S, and then decreases to the south of 25° S (Fig. 9). Honma and Kamimura (1957) have reported a trend toward an increase in sizes of albacore from west to east in the western South Pacific. Though these size differences by area appear to occur regularly, sizes also vary seasonally within the same areas, reflecting seasonal movements of fish. Further studies are necessary before the details of the movement in the South Pacific can be elucidated.

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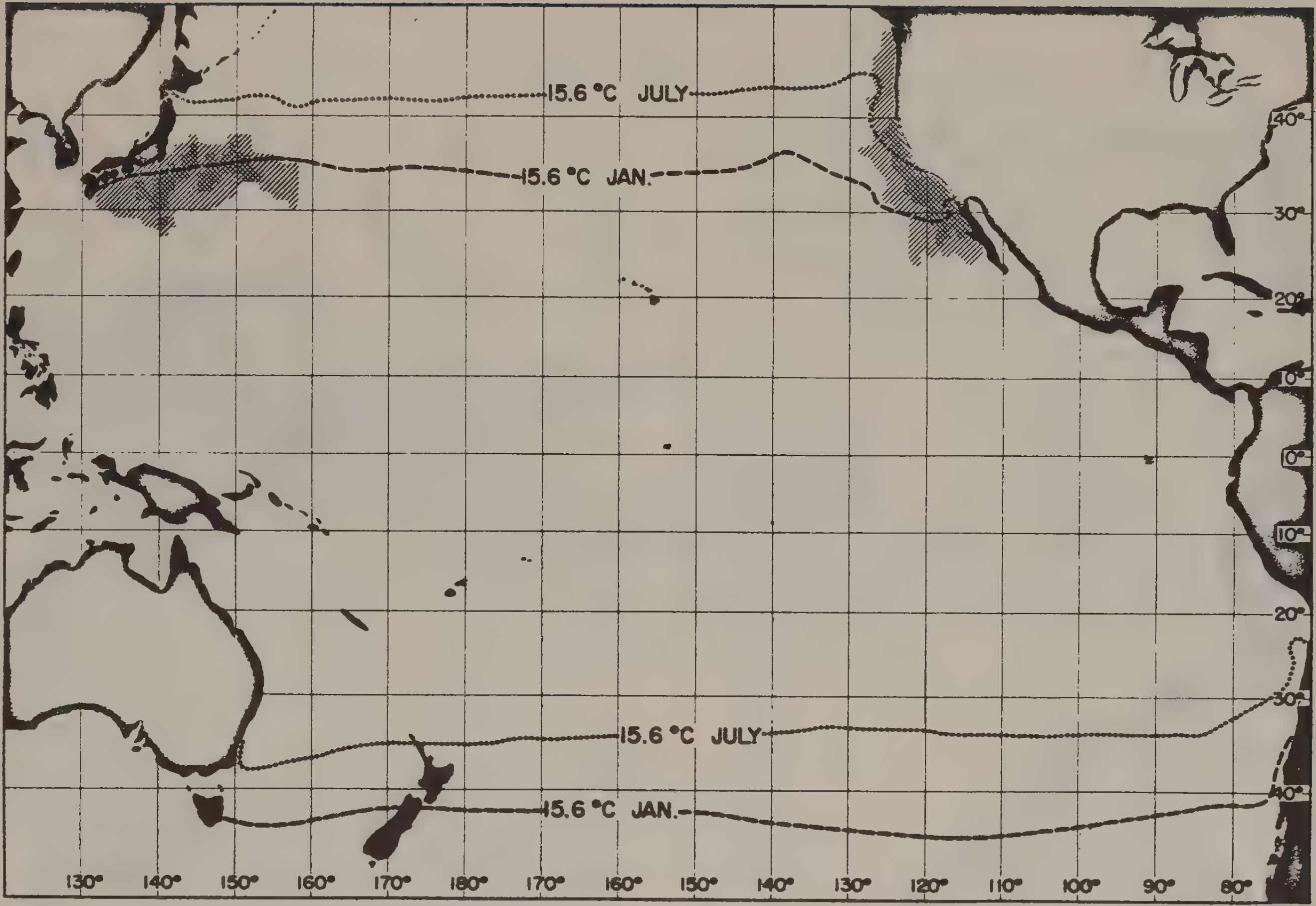
15.6 °C JULY
15.6 °C JAN.
15.6 °C JULY
15.6 °C JAN.
40°
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10°
20°
30°
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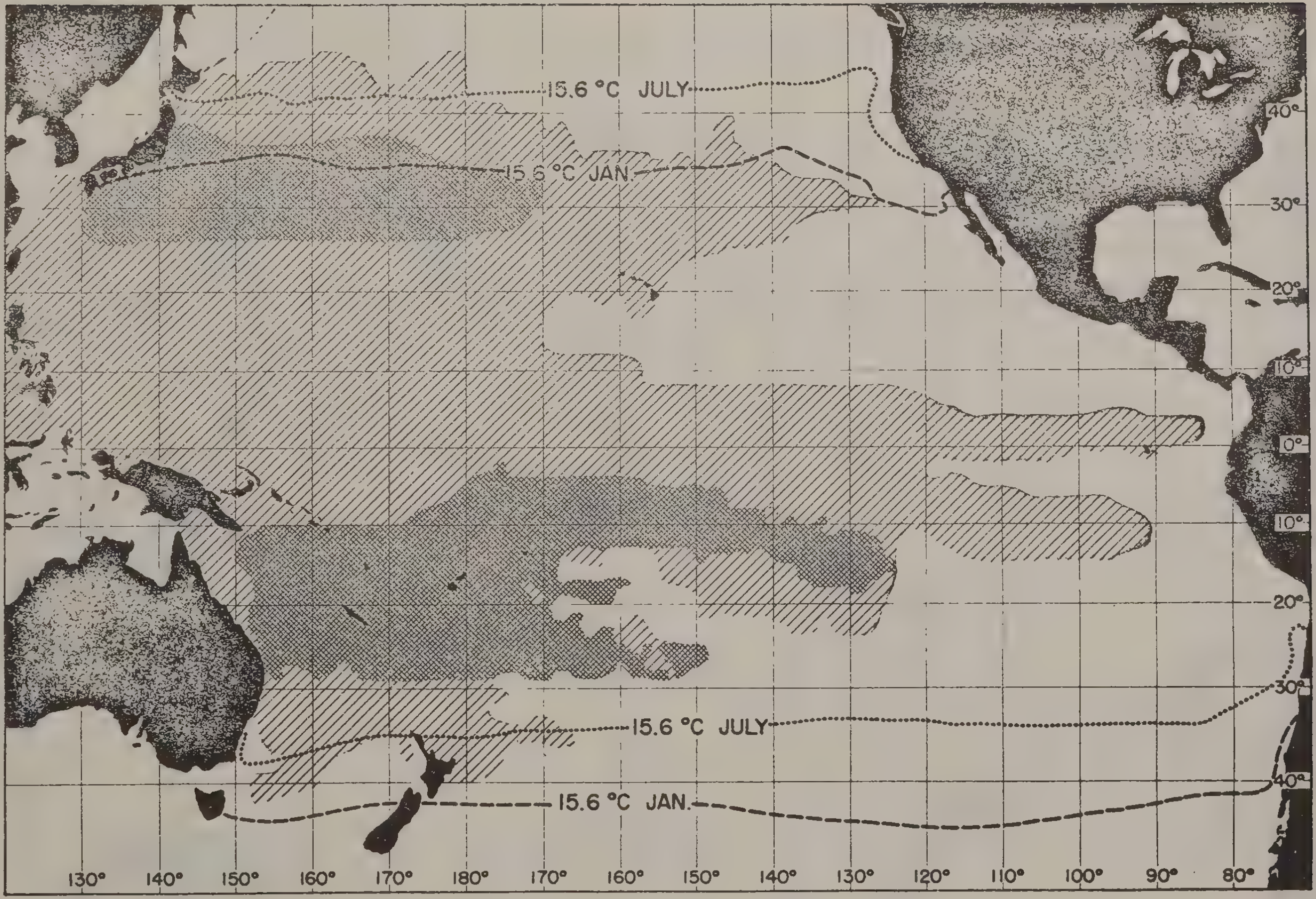
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°

Fig. 1. Surface Fisheries for Albacore in the North Pacific Ocean (Data from Clemens and Craig, 1965; Kawasaki, 1957). The 15.6° Isotherm (for January and July) is Superimposed.


15.6 °C JULY
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40°
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40°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
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120°
110°
100°
90°
80°

Fig. 2. Distribution of Deep-Swimming Albacore (Hatching) and the Principal Fisheries (Crosshatching) in the Pacific Ocean.

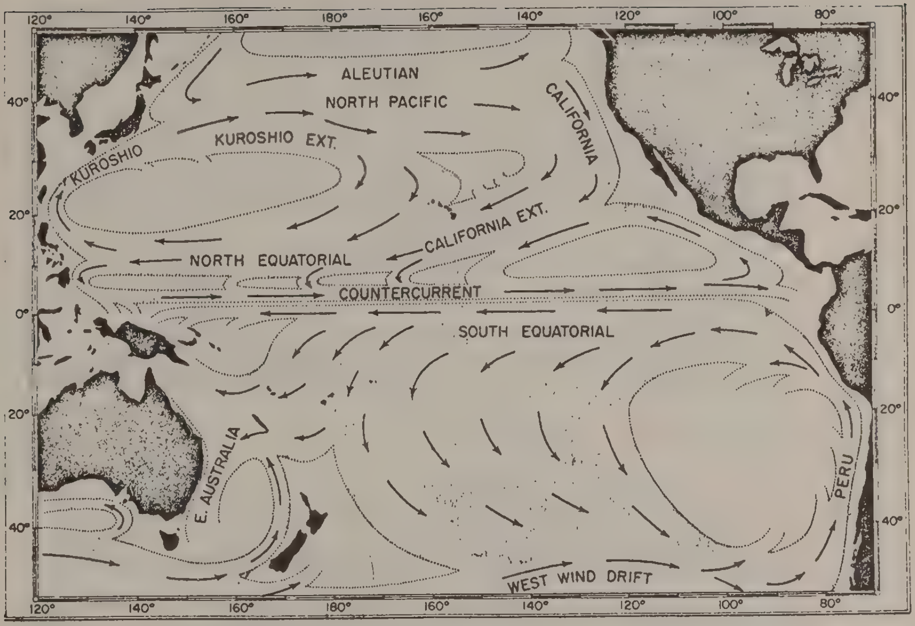
ALEUTIAN
NORTH PACIFIC
KUROSHIO
KUROSHIO EXT.
CALIFORNIA
CALIFORNIA EXT.
NORTH EQUATORIAL
COUNTERCURRENT
SOUTH EQUATORIAL
E. AUSTRALIA
PERU
WEST WIND DRIFT
120°
140°
160°
180°
160°
140°
120°
100°
80°
40°
20°
0°
20°
40°

Fig. 3. Major Current Systems of the Pacific Ocean.

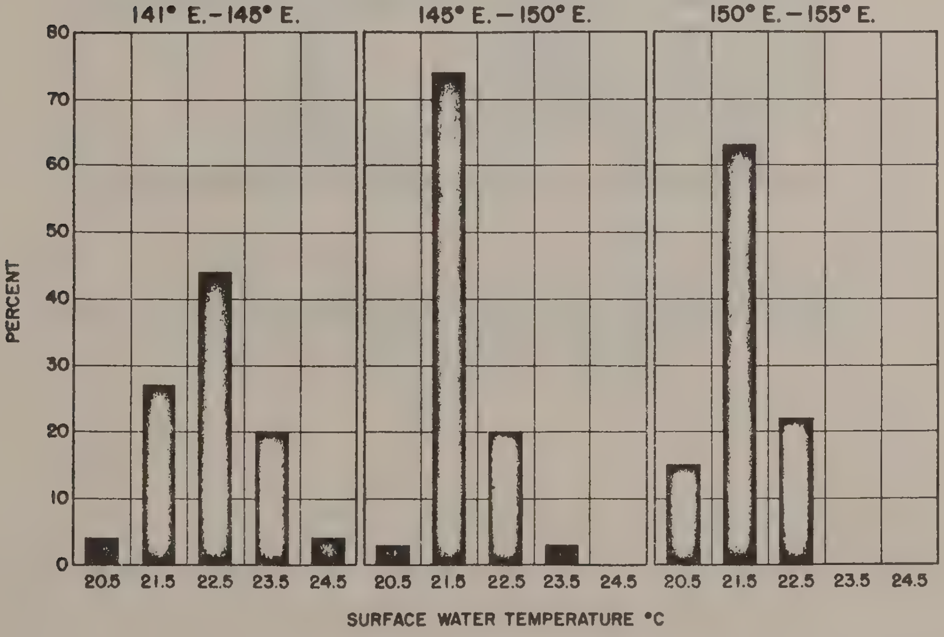

Fig. 4. The Relation Between Albacore Catches, in Weight, and Surface Water Temperature (from Kawasaki and Asano, 1962).

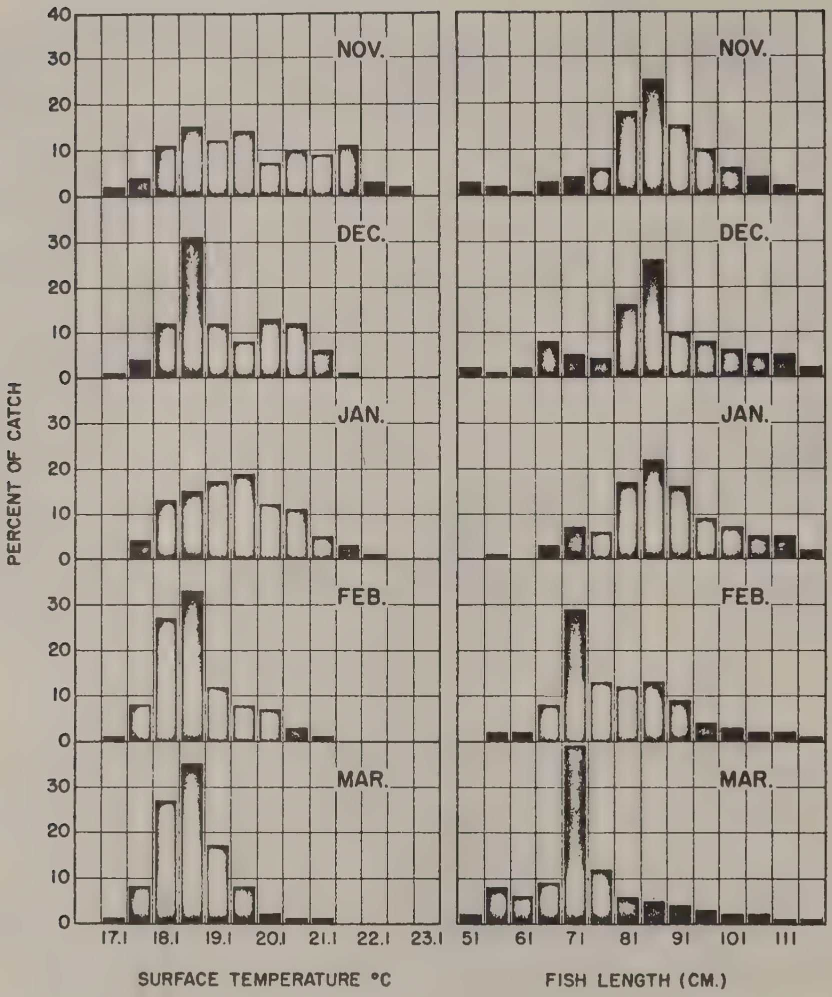

Fig. 5. The Relation Between Water Temperature and Albacore Size and Catches (from Suda and Shiohama, 1962).

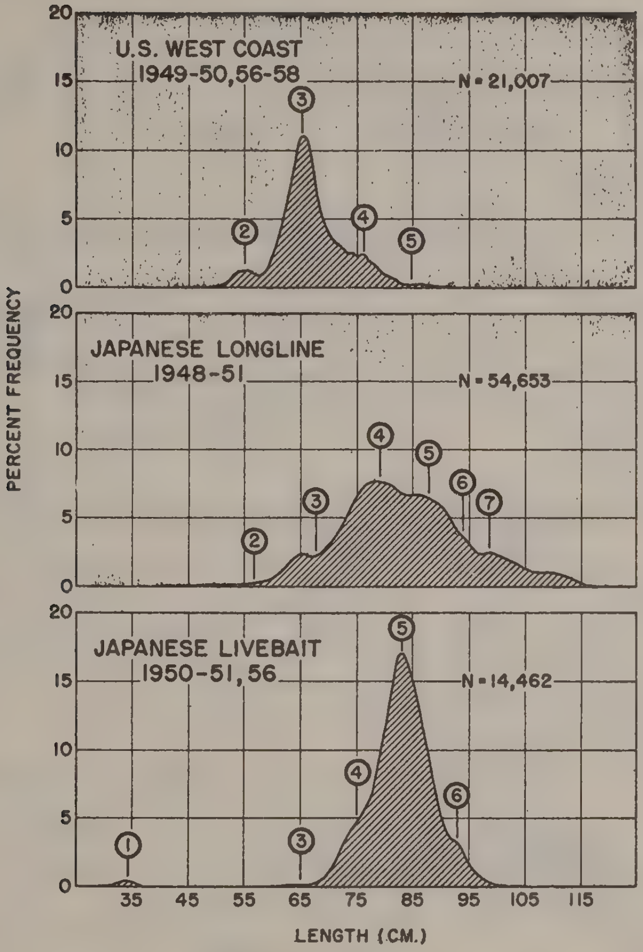

Fig. 6. Composite Length-Frequency Distribution of Albacore Taken in the Three Major North Pacific Fisheries. The Ages (Encircled) are Shown at the Approximate Modal Length of Each Age Group. (Reproduced from Figure 5 of Otsu and Uchida, 1963).

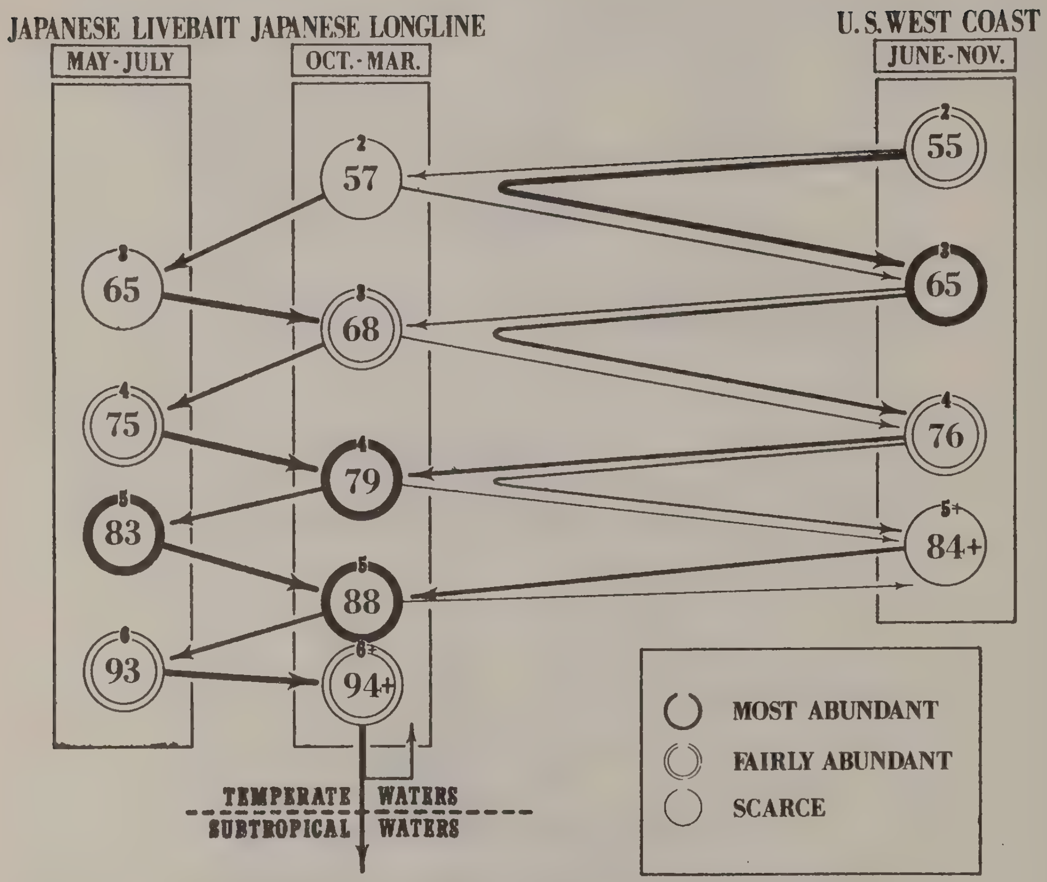
JAPANESE LIVEBAIT
MAY-JULY
JAPANESE LONGLINE
OCT.-MAR.
U.S.WEST COAST
JUNE-NOV.
2
57
3
65
3
68
4
75
4
79
5
83
5
88
6
93
6+
94+
2
55
3
65
4
76
5+
84+
TEMPERATE WATERS
SUBTROPICAL WATERS
MOST ABUNDANT
FAIRLY ABUNDANT
SCARCE

Fig. 7. Diagrammatic Representation of Albacore Migration, by Size (Age) Groups. The Number at the Center of Each Circle Indicates Modal Length (cm); the Smaller Number at the top of the Circle Indicates Age Group. Arrows show Direction of Migration, and the Thickness of the Lines Between Circles Shows Relative Amount of Movement. (Reproduced from Figure 8, Otsu and Uchida, 1963).

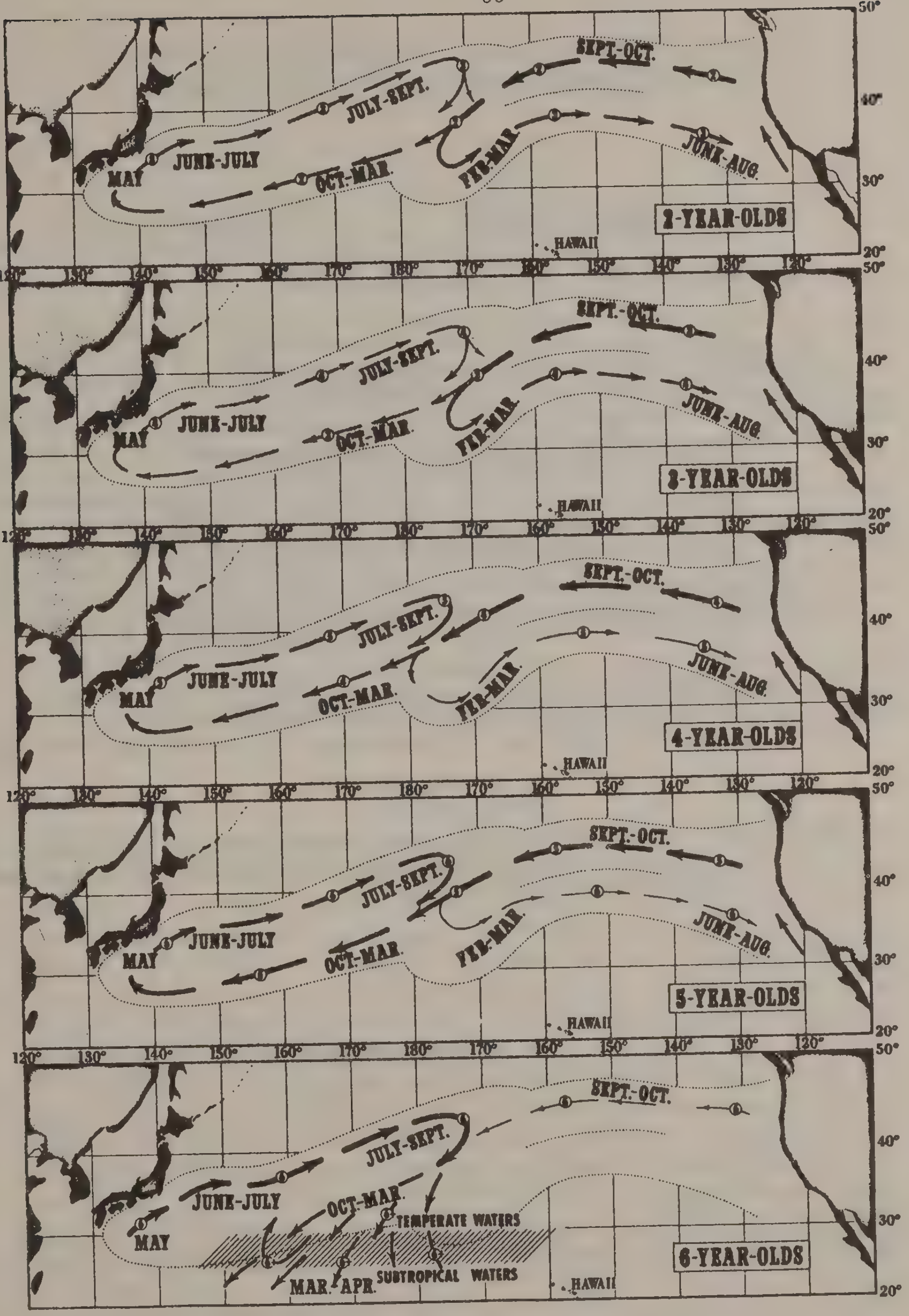
SEPT.-OCT.
JULY-SEPT.
JUNE-JULY
MAY
OCT.-MAR.
FEB.-MAR.
JUNE-AUG.
2-YEAR-OLDS
HAWAII
SEPT.-OCT.
JULY-SEPT.
JUNE-JULY
MAY
OCT.-MAR.
FEB.-MAR.
JUNE-AUG.
3-YEAR-OLDS
HAWAII
SEPT.-OCT.
JULY-SEPT.
JUNE-JULY
MAY
OCT.-MAR.
FEB.-MAR.
JUNE-AUG.
4-YEAR-OLDS
HAWAII
SEPT.-OCT.
JULY-SEPT.
JUNE-JULY
MAY
OCT.-MAR.
FEB.-MAR.
JUNE-AUG.
5-YEAR-OLDS
HAWAII
SEPT.-OCT.
JULY-SEPT.
JUNE-JULY
MAY
OCT.-MAR.
TEMPERATE WATERS
MAR.-APR.
SUBTROPICAL WATERS
6-YEAR-OLDS
HAWAII
120° 130° 140° 150° 160° 170° 180° 170° 160° 150° 140° 130° 120°
50° 40° 30° 20°

Fig. 8. Model of Albacore Migrations in the North Pacific Ocean, by Age Groups (Ages Encircled). (Reproduced from Figure 9, Otsu and Uchida, 1963).

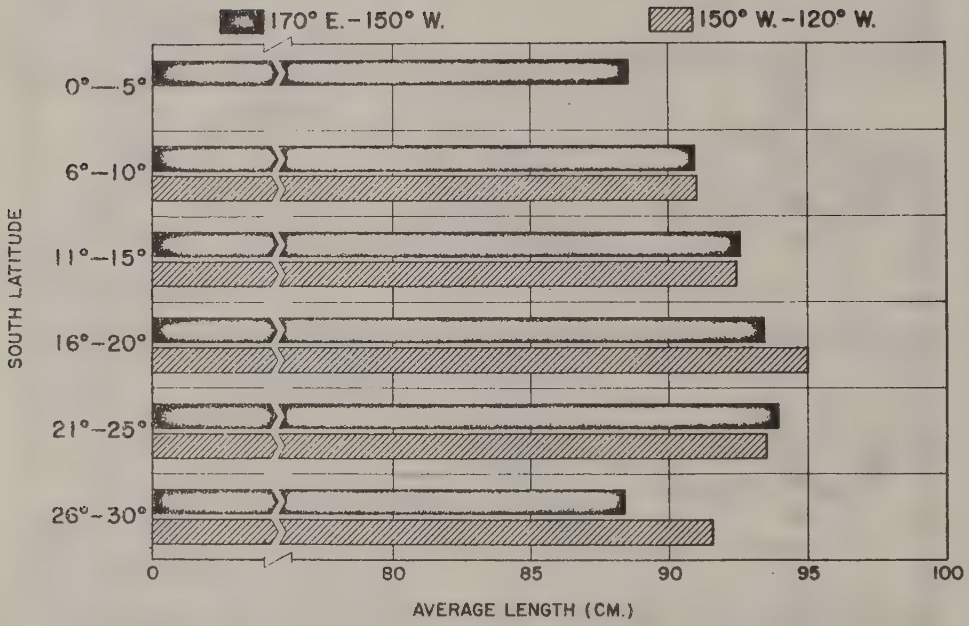

Fig. 9. The Geographical Differences in Average Sizes of Albacore in the South Pacific Ocean (Based on Landings of Samoa-Based Longline Vessels in 1965).

Contributions of Year-Classes of Blue Pike to the Commercial Fishery of Lake Erie, 1943–59[1]

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ABSTRACT

The blue pike (*Stizostedion vitreum glaucum*) contributed about 12.7 million lb annually to the commercial production of fish in Lake Erie in 1915–59. Production averaged about 27% of the total for all species; in some years it exceeded 50%. The catch fluctuated greatly and was featured by a series of seven "highs" and "lows" during the 45-year period. The landings ranged between 2 million and 26 million lb; periods of peak production were 5 to 9 years apart. A sharp decline in the catch started in 1957. The take of 79,000 lb in 1959 was the lowest on record to that time.

Age and size compositions of the catch were determined from samples of blue pike taken from commercial landings in the fall, 1943–59. Peaks in production in that period were attributed to a few strong year-classes separated by several weak year-classes. Of the 20 year-classes represented in the samples, those of 1944 and 1949 were by far the strongest; together they contributed 42% (by weight) of the fall blue pike production in 1943–59. The strength of the 1939 and 1940 year-classes was moderate and the 1954 year-class was the last one of any importance. The other 15 year-classes were weak.

The 1957–59 decline in production was accompanied by a marked increase in rate of growth. Blue pike in age-group III weighed nearly eight times more and were 7.7 inches longer in 1959 than in 1951. Landings after 1958 consisted of only a few large fish. The collapse of the fishery forced blue pike fishermen either to fish for less valuable species or to discontinue operation.

INTRODUCTION

The blue pike (*Stizostedion vitreum glaucum*) has been a most important species in the commercial fishery of Lake Erie; it contributed more than one-fourth of the total catch in 1915–59. The blue pike was valued highly also as a sport fish; in some years, sport catches undoubtedly contributed substantially to the total production. However, changes in recent years have altered the situation entirely. Almost complete lack of recruitment led to record low production in 1958 and 1959. The blue pike fishery is temporarily, perhaps, permanently, in a state of collapse.

The habitat of the blue pike overlaps that of the related subspecies, the walleye (*Stizostedion vitreum vitreum*), in Lake Erie, but the areas of greatest abundance are different. The blue pike is most common in eastern Lake Erie where waters are cool and deep, whereas the walleye is most plentiful in the warm shallow waters of western Lake Erie. The two subspecies are readily separated on the basis of color — blue pike have no yellow pigment; their morphometric differences are too small to be useful for separation of the

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subspecies in the field (Deason, MS, 1936; Stone, MS, 1948). Growth rate was usually much slower in the blue pike than in the walleye (Adamstone, 1922; Deason, 1933).

The present paper is largely a statistical account of the changes in the blue pike fishery, with particular reference to the effects of the strength of various year-classes on the fall fishery. The possible effects of changing biological conditions in the lake on fluctuations in year-class strength are not discussed. Since the species composition of the commercial catches in Lake Erie has changed substantially over the years, it may be assumed that the biological character of the lake also is changing. Fishing methods, gear, and intensity have differed so little over the years in the U.S. waters of the lake that the fishery cannot be held directly accountable for the many changes in production and stocks.

Blue pike production in Lake Ontario, which averaged about 1% of that in Lake Erie, collapsed in 1956 — 2 years before the failure in Lake Erie.

MATERIALS AND METHODS

Scale Collections

Investigations of the contributions of year-classes of blue pike to the fall commercial catch were based on samples of scales and length and weight measurements from 8534 fish; 54 samples were taken from landings at several ports during the fall in 1943–57 (Table I). Samples were not recorded separately by port and gear in 1958 and 1959. Samples of 353 blue pike from Conneaut, Ohio, in April 1951, and 122 at Wheatley, Ontario, in April 1952 are not included in the table but are used for seasonal comparisons of age composition. Gear and numbers of samples taken were: trap nets, 27; gill nets, 26; and pound net, 1. About 50% of all samples were from Conneaut, Ohio, and Erie, Pennsylvania. Others were from Dunkirk, New York; Lorain, Vermilion, and Sandusky, Ohio; and Wheatley, Ontario (Fig. 1).

Trap nets used in Ohio waters had a crib of $2\frac{3}{4}$- to 3-inch mesh (extension measure). Gill-net samples of blue pike prior to 1957 were mostly from gear with meshes of approximately $2\frac{3}{4}$–3 inches, but in 1957–59 most fish, because of their large size, were caught in $4\frac{3}{4}$-inch mesh whitefish nets.

Size of samples and ports of origin varied considerably from year to year. Commercial landings usually were sampled only during a brief period in the fall. Differences in weather conditions and in availability of blue pike at the ports caused a wide variation in the size and geographical distribution of the annual samples.

Total length in inches and weight in ounces were measured for each fish. Scales were removed just above the lateral line below the spiny dorsal fin. Because most blue pike were sold in the round, the fish usually were not opened for determination of sex. All samples were from fish as landed. Undersized fish[2] were included when they occurred in some samples from Ohio because

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[2] The minimum legal length for blue pike was 11 inches in Ohio throughout the period of collection; Pennsylvania and New York had no size limits.

TABLE I. Numbers of blue pike sampled from commercial landings, 1943–59.

Port and gear	Year															Total
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	
Sandusky																
Trap net	–	–	–	117	199	250	–	–	–	166	144	–	–	150	–	1026
Wheatley																
Pound net	–	–	–	–	–	–	–	–	–	–	173	–	–	–	–	173
Gill net	–	–	–	–	–	–	–	–	–	–	–	119	120	157	–	396
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	569
Lorain-Vermilion																
Trap net	122	–	–	–	–	–	160	–	–	–	–	127	104	–	–	513
Gill net	123	73	–	55	107	233	–	–	–	–	124	–	–	151	–	866
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1379
Conneaut																
Trap net	208	85	–	166	342	197	180	136	214	174	–	–	155	156	–	2013
Gill net	–	–	179	–	–	–	–	–	–	–	–	–	–	–	–	179
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2192
Erie																
Trap net	–	–	–	–	–	–	–	–	–	173	125	–	–	149	–	447
Gill net	252	106	221	–	150	233	181	122	–	–	–	147	147	150	128	1837
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2284
Dunkirk																
Trap net	–	–	–	–	–	–	–	–	–	135	–	–	–	153	112	400
Gill net	–	–	–	–	–	–	–	135	–	–	142	50	140	–	–	467
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	867
Grand total	705	264	400	338	798	913	521	393	214	648	708	443	666	1066	240	8534[a]

[a] Includes 108 fish sampled in 1958 and 109 in 1959 which were not separated according to port or gear.

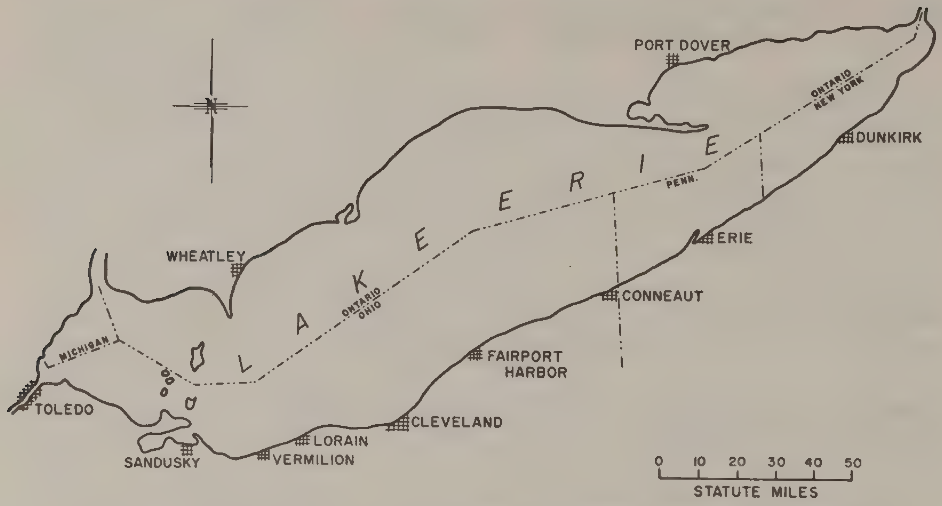
N
PORT DOVER
ONTARIO
NEW YORK
DUNKIRK
LAKE ERIE
PENN.
ERIE
WHEATLEY
ONTARIO
OHIO
CONNEAUT
L. MICHIGAN
FAIRPORT HARBOR
TOLEDO
CLEVELAND
LORAIN
SANDUSKY
VERMILION
0 10 20 30 40 50
STATUTE MILES

FIG. 1. Lake Erie, showing locations where commercial landings were sampled.

they normally were marketed. Ohio permitted the landing of limited quantities of undersized fish.

Ages were determined by counting the annuli on the scales. Although the scales taken in 1943–46 had been examined previously by Frank W. Jobes (Van Oosten, 1948), I read these same scales to ensure consistency of interpretation. The two sets of age determinations agreed closely. A thorough inquiry into the validity of the scale method for age determination of blue pike was not made, but Deason (1933; MS, 1936) presented strong supporting evidence. The validity of the scale method for the closely related walleye was established by Carlander (1945) and Hile (1954). In the present study the persistent strength or weakness of certain year-classes of blue pike in successive calendar years gives additional evidence that age determinations are generally accurate.

SOURCES OF STATISTICS

Production figures for blue pike given in this paper are from Baldwin and Saalfeld (1962) and start with 1915, the first year that the blue pike and walleye were separated in Canadian statistics. Ohio catches of blue pike by month and district and catch per unit of effort are from a summary of the Ohio commercial catch in Lake Erie for 1948–56 and from annual summaries in 1957–59 (Ohio Department of Natural Resources, MS, 1957; MS, 1958; MS, 1959).

PRODUCTION, FISHING INTENSITY, AND AVAILABILITY

PRODUCTION BY STATE AND PROVINCE, 1915–59

The blue pike has been a "money" fish in the Lake Erie fishery since earliest records. Large catches of blue pike were reported as early as 1850, and in 1885 blue pike contributed about 8 million lb to the fishery (Smith and Snell, 1891).

Approximately 571 million lb of blue pike (26.6% of the total production of all species) were taken in the commercial fishery in Lake Erie by the United States and Canada in 1915–59 (Table II). Blue pike contributed more than 50% of the total catch in 1936, 1943, and 1944, and between 40 and 50% in 1930, 1937, and 1949.

The commercial catch of blue pike exhibited extreme fluctuations. Production from 1915 to 1957 included a series of highs and lows ranging between extremes of 26 million and 2 million lb, with peaks from 5 to 9 years apart (Fig. 2). The catch of 1,400,000 lb in 1958 was the lowest on record up to that time, and production in 1959 of only 79,000 lb marked the collapse of the fishery.[3]

Despite extreme fluctuations, total catches of blue pike showed no distinct trends except for the extremely sharp decline in production which began in 1958. Mean annual production in 1915–59 was 12,681,000 lb (Table III). The highest mean annual production for shorter periods was 16,575,000 lb in 1930–39 and the lowest was 8,761,000 lb in 1915–19. Despite the low production in 1958 and 1959, the average annual take for 1950–59 was only 1 million lb below the 45-year average.

Catches of blue pike in the United States and Canada, considered separately, have shown definite trends since 1915. Average annual U.S. production by periods increased from 6,529,000 lb in 1915–19 to 10,971,000 lb in 1930–39 and then decreased to 4,849,000 lb in 1950–59, whereas average annual Canadian production increased steadily (except in 1940-49) from 2,232,000 lb in 1915–19 to 6,958,000 lb in 1950–59. Much of the rise in Canadian production, particularly after 1949, was caused by increased fishing intensity. This increase was caused primarily by the introduction of nylon gill nets in 1949–50. The United States contributed 60 to 74% of the total blue pike production during the periods prior to 1950, but only 41% in 1950–59. The range of the percentage contribution of annual U.S. production to the lakewide total was 35 (1951) to 79 (1915); the 45-year average was 61.

The differences in trend make it difficult to judge the degree of similarity of short-term fluctuations in the production of blue pike in the U.S. and Canada. To permit better comparisons, trend lines were fitted to the production data for 1915–35 and 1936–56 in the U.S. and for 1915–56 in Canada. Deviations of the respective annual catches from the trend lines for the U.S. and Canadian production had a highly significant positive correlation ($r = 0.650$; $p = 0.001$; df = 40)—a strong indication that the U.S. and Canadian fishermen exploited common stocks of blue pike.

The percentage contributions of Ohio, Pennsylvania, and New York to the U.S. catch of blue pike have shown no clear trend (Table IV). The average percentages of U.S. production landed in these states in 1915–59 were Ohio,

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[3] Annual catches in pounds of blue pike in Lake Erie in 1960–64 were: 1960—12,000; 1961—3000; 1962—1000; 1963—<500; 1964—<500.

TABLE II. Commercial production (thousands of pounds) of blue pike in Lake Erie, 1915–59.[a]

Year	United States				Canada: Ontario	Lake total
	Ohio	Pennsylvania	New York	Total		
1915	13,079	4,796	886	18,761	4,882	23,643
1916	7,683	1,408	298	9,381	2,539	11,920
1917	1,499	88	18	1,605	566	2,710
1918	1,069	79	75	1,222	785	2,007
1919	1,532	80	63	1,675	2,388	4,063
1920	3,494	302	169	3,965	3,355	7,319
1921	5,836	2,741	367	8,944	6,367	15,311
1922	7,202	2,593	565	10,359	6,313	16,672
1923	6,028	3,013	642	9,683	3,194	12,877
1924	5,363	3,077	527	8,967	2,988	11,955
1925	4,047	–	–	10,478	3,330	13,808
1926	4,234	2,936	2,170	9,340	2,975	12,315
1927	4,637	2,190	475	7,301	3,078	10,379
1928	3,743	627	449	4,819	2,104	6,923
1929	1,803	713	305	2,820	2,538	5,359
1930	9,017	2,211	564	11,792	5,898	17,691
1931	7,849	3,690	1,103	12,643	5,358	18,001
1932	7,784	1,607	475	9,867	3,962	13,829
1933	6,735	1,747	304	8,786	4,152	12,938
1934	5,765	2,132	459	8,356	2,298	10,654
1935	7,142	2,084	460	9,686	5,064	14,750
1936	16,447	2,837	624	19,909	6,879	26,788
1937	7,020	2,304	1,638	10,961	9,355	20,316
1938	6,154	1,442	1,064	8,659	7,158	15,817
1939	7,263	1,257	529	9,049	5,911	14,960
1940	4,541	313	97	4,951	2,012	6,963
1941	3,029	217	33	3,287	1,544	4,831
1942	5,296	824	98	6,222	4,405	10,627
1943	8,055	2,364	809	11,228	9,614	20,842
1944	11,278	2,129	1,526	14,933	9,390	24,323
1945	5,167	1,762	843	7,772	6,559	14,331
1946	2,550	351	111	3,012	1,909	4,921
1947	2,896	145	78	3,120	1,646	4,766
1948	6,957	1,473	553	9,003	5,742	14,745
1949	10,616	2,479	905	14,000	9,784	23,783
1950	4,900	1,112	178	6,190	8,611	14,801
1951	1,867	174	109	2,150	3,914	6,064
1952	5,531	1,081	158	6,771	7,267	14,038
1953	6,853	924	265	8,042	10,333	18,375
1954	4,576	1,349	319	6,245	8,151	14,396
1955	3,679	2,335	1,634	7,648	12,037	19,685
1956	4,703	1,231	921	6,855	12,002	18,857
1957	2,915	629	437	3,981	6,389	10,370
1958	366	74	136	576	824	1,399
1959	20	5	7	32	47	79

[a]Data are from Baldwin and Saalfeld (1962). Records are not available for production in Pennsylvania and New York in 1925. Michigan production (included in U.S. and Lake totals) was less than 500 pounds except for the following years: 1941—8000 lb; 1942—4000; 1946 and 1947—1000; and 1948—20,000.

69; Pennsylvania, 21; and New York, 10. Periods of highest mean annual production were Ohio, 8,118,000 lb in 1930–39; Pennsylvania, 2,219,000 lb in 1920–29; New York, 1,505,000 lb in 1940–49.

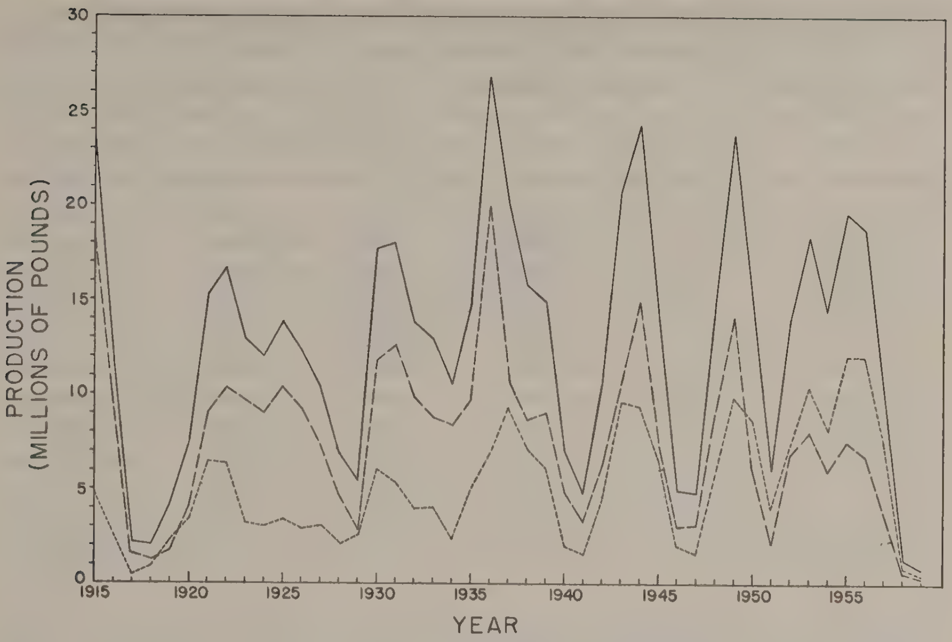

FIG. 2. Commercial production of blue pike in Lake Erie, 1915–59. Province of Ontario, short dashes; United States, long dashes; and Lake Erie total, solid line.

TABLE III. Average annual production (thousands of pounds) of blue pike in U.S. and Canadian waters of Lake Erie during different periods in 1915–59. (Percentages of total catch of blue pike in parentheses.)

Period	Number of years	United States	Canada	Total
1915–19	5	6,529	2,232	8,761
		(74)	(26)	
1920–29	10	7,668	3,624	11,292
		(68)	(32)	
1930–39	10	10,971	5,604	16,575
		(66)	(34)	
1940–49	10	7,753	5,261	13,014
		(60)	(40)	
1950–59	10	4,849	6,958	11,807
		(41)	(59)	
1915–59	45	7,667	5,014	12,681
		(61)	(39)	

The most productive blue pike fishery in the U.S. was in Ohio east of and including Fairport Harbor, where nearly 63% of the state's blue pike were produced in 1956–59. About 95% of the Ohio catch in 1948–59 was taken in

TABLE IV. Average annual production (thousands of pounds) of blue pike in Ohio, Pennsylvania, and New York and (in parentheses) percentage contributions of each to the U.S. total in Lake Erie during different periods in 1915–59.

Period	Number of years	Ohio	Pennsylvania	New York	Total[a]
1915–19	5	4,972 (76)	1,290 (20)	266 (4)	6,529
1920–29	10	4,639 (60)	2,219 (29)	810 (11)	7,668
1930–39	10	8,118 (74)	2,131 (19)	722 (7)	10,971
1940–49	10	6,039 (78)	1,206 (16)	505 (6)	7,753
1950–59	10	3,541 (73)	891 (18)	416 (9)	4,849
1915–59	45	5,516 (69)	1,576 (21)	575 (10)	7,667

[a] Includes Michigan catches, none of which exceeded 0.5% of the total catch in any period.

trap nets, and more than half (58%) of the U.S. production in the same years was in May and June, the spawning months for this species.

RELATION BETWEEN PRODUCTION AND AVAILABILITY

Knowledge of the general relation between production and the availability or abundance of blue pike in Lake Erie is most important to an understanding of data presented in later sections. Regrettably, useful statistics on catch per unit of effort are lacking for some waters of Lake Erie and are incomplete for others. The actual contributions of the year-classes to the commercial landings can be estimated with fair precision, but interpretation of these estimates in terms of year-class strength requires some assurance that fluctuations of catch and abundance are similar.

The continuing collection of catch-effort statistics was started in New York and Pennsylvania in 1950. Because of the changes in the blue pike population that began shortly after the middle of the decade, the period for which usable statistics are available is too short for a study of the relation between production and catch per unit of effort. The catch in gill nets (the dominant gear in these two states) was affected particularly by the increase in mesh size that accompanied the increase in size of blue pike.

The situation is considerably better in Ohio, where records of total effort and catch start with 1948. Helpful, also, is the fact that such a high proportion of the Ohio catch of blue pike was produced by trap nets, a gear little affected by changes in size composition. Further discussion in this section is based entirely, therefore, on the Ohio trap-net statistics.

The Ohio statistics have two shortcomings. The effort is in terms of the total number of trap nets lifted rather than the number of lifts in which blue pike were caught (the "effective fishing effort" described by Hile, 1962); and the recorded lifts are for all Ohio waters, although relatively few blue pike were taken in the westernmost of the three statistical districts, usually for only a short period in the fall. I believe, however, that neither defect is highly damaging. When blue pike were present in considerable numbers they were taken daily by trap netters in most of the central and all of the eastern district; thus the total fishing effort and the effective fishing effort for blue pike in these waters must have been nearly identical. The charging of fishing effort from the western district against blue pike does offer a source of bias, but estimates of fluctuations in availability would not be affected adversely unless the percentage of the total lifts made in the western district fluctuated substantially from year to year. I found no evidence of any great differences among the districts in the trends of fishing pressure and believe, therefore, that the catch per trap-net lift, computed from the total production of blue pike in trap nets and the total number of lifts in all Ohio waters, offers a reasonably dependable measure of annual fluctuations in the availability of blue pike in Ohio.

Fluctuations in the total production of blue pike in Ohio waters sometimes were greater than were those in the catch per trap-net lift but they agreed in showing a strong though irregular downward trend (Table V, Fig. 3). There is some evidence that the progressive downward shift in production may be attributed to the fairly consistent downward trend in fishing effort.

Despite certain disagreements between the curves of production and catch per unit of effort, either curve would have led to much the same conclusions regarding annual fluctuations in the abundance of blue pike. The

TABLE V. Production (thousands of pounds) of blue pike taken by trap nets, total number of trap-net lifts, and catch of blue pike per lift in Ohio waters of Lake Erie, 1948–58.

Year	Production	Number of lifts	Pounds per lift
1948	6,726	187,363	35.9
1949	10,259	169,006	60.7
1950	4,735	151,291	31.3
1951	1,817	144,180	12.6
1952	5,430	162,470	33.4
1953	6,435	136,629	47.1
1954	4,343	136,570	31.8
1955	3,423	106,956	32.0
1956	4,265	107,155	39.8
1957	2,611	110,620	23.6
1958	323	99,660	3.2

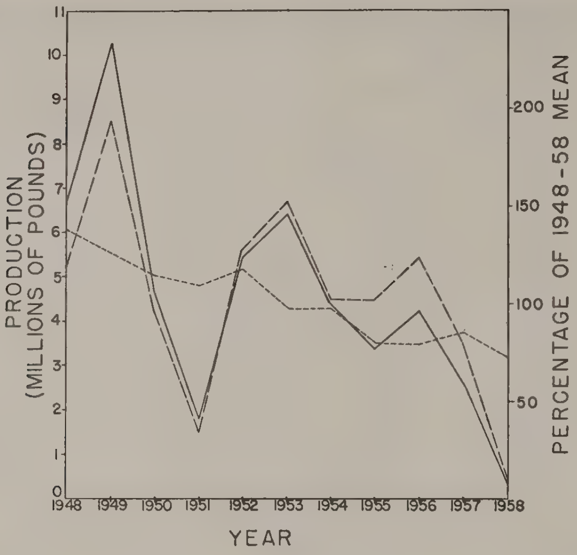

FIG. 3. Production of blue pike (solid line), fishing intensity (short dashes), and catch per trap net lift (long dashes) in the commercial trap-net fishery of the Ohio waters of Lake Erie, 1948–58. Scale at left applies to production only; scale at right applies to all three variables.

coefficient of correlation between the two sets of values was high ($r = 0.947$; $p = 0.001$; df $= 9$). It cannot be assumed that a similar relation between catch and availability existed in all blue pike fisheries, but the finding for the important trap-net fishery of Ohio lends confidence in the use of production statistics to judge changes of abundance in sections of Lake Erie where data on catch per unit of effort are not available.

That fluctuations of catch and availability of blue pike in the Ohio trap-net fishery are closely similar is in agreement with the opinions and findings of other investigators. Doan (1942) held that catch records for Lake Erie species, though not perfect measures, did reflect well all major changes of abundance. He reproduced figures from Hile (1937) in support of his view that catch and catch per unit of effort were correlated closely. A similar observation was made by Van Oosten et al. (1946).

AGE COMPOSITIONS, LENGTHS, AND WEIGHTS

VARIABILITY OF SAMPLES BY PORT, SECTION OF LAKE, AND GEAR

A study of the contributions of year-classes to the commercial fishery calls first for an inquiry into the variability of ages and weights of blue pike sampled from different ports, sections of the lake, seasons of the year, and by different gears. This information is essential if data are to be combined or stratified to obtain the most dependable description of changes in the fishery.

The numbers of fish, age composition, types of gear, and average age, length, and weight of blue pike in fall samples from landings at different ports in 1943–59 are recorded in Table VI. Studies of the variability of mean ages, lengths, and weights are handicapped somewhat by year-to-year differences in port and gear. Continuous samples were not taken at any single port, and landings were sampled only from gill nets in 1945 and only from trap nets in 1951 and 1952.

To evaluate possible bias from port and gear of capture, the materials of Table VI were grouped by paired samples as listed in Table VII. The first line in the body of Table VII shows, for example, that a sample of blue pike taken by gill nets from a particular port averaged 0.3 year older and 0.1 oz lighter (16 comparisons) than samples taken farther west in the same year. (In this analysis a port not at the extreme eastern or western end of the lake can serve alternatively as "easterly" and "westerly.") Samples from trap nets yielded similar results; on the average (21 comparisons), fish from a particular port averaged 0.2 year older and 0.9 oz lighter than those in samples collected farther west.

Since data were lacking for a comparison of gill-net and trap-net samples collected in the same year at the same port, comparison was based on records from the closely adjacent gill-net grounds of Erie and trap-net grounds of Conneaut. Here the gill-net fish averaged 0.1 year older and 1.0 oz heavier than the trap-net fish (eight comparisons). The broader comparison (24 pairs) of gill-net and trap-net samples from all ports yielded the slightly greater difference ot 0.2 year and 1.1 oz.

Table VII gives clear evidence that the mean age and weight of samples of blue pike from Lake Erie are influenced by port and gear of capture. Yet this bias is not great enough to be highly damaging when considered in relation to the actual average ages and weights of the different samples (Table VI). Consequently, all available collections for each year are employed, without separation according to port or gear, in later analyses of data on the strength and contribution of year-classes.

The collection of most of the samples in the fall raises the further question whether the data on year-class composition from fall samples are applicable the following spring. Since overwinter growth almost surely is inconsequential or nil and hence no significant recruitment of catchable-sized fish can take place, growth cannot change greatly the year-class composition and the size of blue pike in the fishery from the fall to the following spring. Questions exist, however, whether natural mortality, late fall and winter fishing mortality,[4] or seasonal differences in segregation by size and maturity of blue pike could impair the applicability of data from fall collections to analyses of data on the fishery of the following spring.

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[4] In the years that scale samples were taken (1943–59), commercial fishing was open in all waters of Lake Erie except from December 21 to March 14 in Ohio, and January 1 to March 10 in Michigan. Even when fishing was legal, bad weather and ice greatly reduced fishing effort in late December through February.

TABLE VI. Percentages of total numbers of blue pike contributed by different age-groups in samples from commercial catches in the fall, and average ages, lengths, and weights of fish in the samples, Lake Erie, 1943–59. (The percentage of the total weight of the annual samples contributed by each age-group is given in parentheses. Asterisks indicate modes.)

			Age-group[b]								Grand average		
Year and port	Gear[a]	No. of fish	I	II	III	IV	V	VI	VII	VIII	Age[c]	Length (*inches*)	Weight (*ounces*)
1943													
Conneaut	T	208	–	0.5	43.7	55.3	0.5	–	–	–	3.6	11.8	8.3
Lorain	T	122	0.8	6.6	31.1	56.6	4.9	–	–	–	3.6	12.9	11.0
Erie	G	252	–	0.8	37.7	59.9	1.6	–	–	–	3.6	12.1	8.9
Vermillon	G	123	–	–	35.8	63.4	0.8	–	–	–	3.6	12.4	9.6
Total or		705	0.1	1.6	38.0	58.6*	1.7	–	–	–	3.6	12.2	9.2
average			(0.1)	(1.3)	(36.3)	(60.0)	(2.3)	–	–	–	–	–	–
1944													
Conneaut	T	85	2.4	10.6	5.9	56.5	24.6	–	–	–	3.9	12.7	10.5
Erie	G	106	–	–	3.8	67.9	28.3	–	–	–	4.2	12.7	10.6
Lorain	G	73	–	24.6	15.1	48.0	12.3	–	–	–	3.4	13.2	12.0
Total or		264	0.8	10.2	7.6	58.7*	22.7	–	–		3.9	12.8	11.0
average			(0.4)	(9.5)	(7.3)	(59.1)	(23.7)	–	–	–	–	–	–
1945													
Erie	G	221	–	3.2	4.5	54.3	31.2	6.8	–	–	4.3	13.4	11.2
Conneaut	G	179	0.6	37.4	11.7	29.6	19.6	1.1	–	–	3.3	12.3	8.4
Total or		400	0.3	18.5	7.7	43.3*	26.0	4.2	–	–	3.9	12.9	9.9
average			(0.2)	(12.6)	(6.9)	(45.0)	(30.2)	(5.1)	–	–	–	–	–
1946													
Conneaut	T	166	–	42.2	21.7	12.6	17.5	6.0	–	–	3.2	12.3	8.1
Sandusky	T	117	–	91.7	8.3	–	–	–	–	–	2.1	11.6	6.9
Lorain	G	55	–	21.8	25.4	31.0	20.0	1.8	–	–	3.5	14.1	13.4
Total or		338	–	56.0*	17.7	11.3	11.8	3.2	–	–	2.7	12.3	8.5
average			–	(49.0)	(15.8)	(12.8)	(17.0)	(5.4)	–	–	–	–	–
1947													
Conneaut	T	342	–	7.6	88.3	2.9	0.6	0.6	–	–	3.0	11.7	7.6
Sandusky	T	199	–	4.0	91.0	5.0	–	–	–	–	3.0	12.5	8.7
Erie	G	150	–	23.3	59.4	11.3	6.0	–	–	–	3.0	11.6	7.0
Lorain	G	107	–	7.5	78.5	8.4	3.7	1.9	–	–	3.1	12.7	9.1
Total or		798	–	9.7	82.2*	5.7	1.9	0.5	–	–	3.0	12.1	8.0
average			–	(9.7)	(77.6)	(8.2)	(3.4)	(1.1)	–	–	–	–	–

1948													
Conneaut	T	197	–	–	2.5	97.0	0.5	–	–	–	4.0	11.7	8.0
Sandusky	T	250	–	–	6.4	90.8	1.6	0.8	0.4	–	4.0	12.8	10.5
Erie	G	233	–	–	2.6	94.4	3.0	–	–	–	4.0	11.9	8.4
Lorain	G	233	–	–	3.4	92.3	4.3	–	–	–	4.0	12.8	10.3
Total or		913	–	–	3.8	93.5*	2.4	0.2	0.1	–	4.0	12.4	9.4
average			–	–	(3.2)	(93.9)	(2.5)	(0.2)	(0.2)	–	–	–	–
1949													
Conneaut	T	180	–	–	1.1	11.1	86.1	1.7	–	–	4.9	12.2	8.6
Lorain	T	160	–	1.9	–	3.1	90.0	4.4	0.6	–	4.9	13.1	11.2
Erie	G	181	–	–	–	2.8	93.9	2.8	0.5	–	5.0	12.1	8.8
Total or		521	–	0.6	0.4	5.7	90.0*	2.9	0.4	–	4.9	12.4	9.5
average			–	(0.4)	(0.2)	(5.2)	(90.7)	(3.1)	(0.4)	–	–	–	–
1950													
Conneaut	T	136	1.5	1.5	3.0	27.9	44.8	21.3	–	–	4.8	12.3	8.3
Dunkirk	G	135	0.7	0.7	0.7	8.1	22.3	63.8	3.0	0.7	5.6	13.6	12.0
Erie	G	122	0.8	–	1.6	7.4	48.4	36.1	5.7	–	5.3	13.5	11.3
Total or		393	1.0	0.8	1.8	14.7	38.2	40.4*	2.8	0.3	5.2	13.1	10.5
average			(0.5)	(1.0)	(3.3)	(27.4)	(34.7)	(31.8)	(1.0)	(0.3)	–	–	–
1951													
Conneaut	T	214	–	8.9	9.8	21.5	34.5*	21.0	4.3	–	4.6	11.9	7.9
			–	(5.6)	(7.3)	(16.8)	(34.7)	(27.9)	(7.7)	–	–	–	–
1952													
Dunkirk	T	135	–	3.0	80.8	8.1	7.4	0.7	–	–	3.2	11.3	6.6
Erie	T	173	–	2.9	87.8	6.4	0.6	1.7	0.6	–	3.1	11.9	8.2
Conneaut	T	174	–	5.7	86.8	7.5	–	–	–	–	3.0	11.4	6.9
Sandusky	T	166	–	1.8	80.7	17.5	–	–	–	–	3.2	12.5	8.8
Total or		648	–	3.4	84.2*	9.9	1.8	0.6	0.1	–	3.1	11.8	7.7
average			–	(3.2)	(82.6)	(10.0)	(2.1)	(1.4)	(0.7)	–	–	–	–
1953													
Erie	T	125	–	3.2	17.6	72.8	3.2	1.6	–	1.6	3.9	12.3	8.2
Wheatley	P	173	–	1.7	21.5	67.4	5.9	2.9	0.6	–	3.9	11.5	7.9
Sandusky	T	144	–	2.1	4.9	90.2	2.8	–	–	–	4.0	12.8	10.3
Dunkirk	G	142	1.4	2.1	17.6	74.0	2.8	0.7	–	1.4	3.8	11.1	6.5
Lorain	G	124	–	0.8	9.7	86.3	3.2	–	–	–	3.9	12.5	8.8
Total or		708	0.3	2.0	14.6	77.7*	3.8	0.9	0.1	0.6	3.9	12.2	8.3
average			(0.1)	(1.6)	(13.3)	(76.9)	(4.0)	(1.7)	(0.2)	(2.2)	–	–	–

(*Continued*)

TABLE VI. Percentages of total numbers of blue pike contributed by different age-groups in samples from commercial catches in the fall, and average ages, lengths, and weights of fish in the samples, Lake Erie, 1943–59. (The percentage of the total weight of the annual samples contributed by each age-group is given in parentheses.) — (*Concluded*)

Year and port	Gear[a]	No. of fish	Age-group[b]								Grand average		
			I	II	III	IV	V	VI	VII	VIII	Age[c]	Length (*inches*)	Weight (*ounces*)
1954													
Lorain	T	127	0.2	64.8	12.7	6.4	15.9	–	–	–	2.7	12.8	10.4
Dunkirk	G	50	–	–	8.0	34.0	58.0	–	–	–	4.5	13.4	12.1
Erie	G	147	–	6.8	16.3	49.7	27.2	–	–	–	4.0	12.4	10.5
Wheatley	G	119	2.5	20.1	12.6	26.9	36.3	1.6	–	–	3.8	12.6	10.8
Total or		443	1.1	26.0	13.3	29.3	29.8*	0.5	–	–	3.6	12.7	10.7
average			(1.0)	(22.2)	(13.1)	(29.3)	(33.9)	(0.5)	–	–	–	–	–
1955													
Conneaut	T	155	12.3	7.7	21.9	27.7	20.0	9.7	0.6	–	3.7	14.3	17.3
Vermillon	T	104	18.3	15.4	39.4	7.7	6.7	12.5	–	–	3.1	14.9	19.5
Dunkirk	G	140	8.6	11.4	10.0	23.6	33.6	12.1	0.7	–	4.0	14.7	19.8
Erie	G	147	10.9	16.3	23.1	27.2	21.8	0.7	–	–	3.4	14.2	17.2
Wheatley	G	120	8.3	14.2	39.2	12.5	14.2	11.6	–	–	3.4	14.3	17.8
Total or		666	11.4	12.7	25.5*	20.9	20.1	9.1	0.3	–	3.5	14.4	18.2
average			(4.9)	(9.0)	(22.8)	(22.2)	(27.3)	(13.5)	(0.3)	–	–	–	–
1956													
Dunkirk	T	153	3.3	85.6	–	0.7	2.6	5.2	2.6	–	2.4	12.9	12.8
Erie	T	149	4.7	83.3	1.3	2.7	–	2.0	6.0	–	2.4	12.7	11.7
Conneaut	T	156	4.5	92.9	0.7	1.9	–	–	–	–	2.0	12.5	10.5
Sandusky	T	150	9.3	89.4	1.3	–	–	–	–	–	1.9	12.8	11.3
Erie	G	150	0.7	89.2	2.0	0.7	2.0	2.7	2.0	0.7	2.3	13.0	12.5
Vermilion	G	151	–	98.7	1.3	–	–	–	–	–	2.0	12.6	11.1
Wheatley	G	157	–	97.4	2.6	–	–	–	–	–	2.0	12.9	12.0
Total or		1066	3.2	91.0*	1.3	0.9	0.7	1.4	1.4	0.1	2.1	12.8	11.7
average			(2.4)	(85.1)	(1.4)	(2.2)	(1.6)	(3.1)	(3.9)	(0.3)	–	–	–
1957													
Erie	G	128	–	63.2	35.2	0,8	–	–	0.8	–	2.4	15.1	22.8
Dunkirk	T	112	3.6	58.8	25.0	2.7	1.8	4.5	0.9	2.7	2.7	14.8	19.2
Total or		240	1.7	61.2*	30.4	1.7	0.8	2.1	0.8	1.3	2.5	15.0	21.1
average			(0.9)	(52.6)	(32.7)	(2.9)	(2.0)	(5.1)	(1.5)	(2.3)	–	–	–
1958													
Several ports	T, G	109	–	3.7	42.2*	25.7	9.2	9.2	7.3	1.8	4.1	18.4	44.5
			–	(1.6)	(36.1)	(24.1)	(12.8)	(10.8)	(9.3)	(4.5)	–	–	–
1959													
Several ports	T, G	108	0.9	–	19.4	46.3*	10.2	9.3	9.3	3.7	4.5	19.8	60.5
			(0.4)	–	(14.9)	(37.8)	(11.6)	(11.1)	(15.2)	(7.0)	–	–	–

[a] T = trap net, G = gill net, P = pound net.

[b] No fish of age-group IX were collected; fish of age-group X were taken only in 1958 (0.9% of the number and 0.8% of the weight) and in 1959 (0.9% of the number and 2.0% of the weight).

[c] Average number of annuli; an additional growing season had been practically completed at the time of collection.

TABLE VII. Differences in average age (numbers of completed annuli) and weight (ounces) as determined from various groupings of paired samples. (Both samples of each pair were collected in the same year; table is based on data of Table VI.)

Basis of comparison	Number of paired samples	Mean difference between averages[a]	
		Age	Weight (*ounces*)
Easterly and westerly[b] ports (gill nets)	16	0.3	-0.1
Easterly and westerly ports (trap nets)	21	0.2	-0.9
Gill nets (Erie) and trap nets (Conneaut)	8	0.1	1.0
Gill nets (all ports) and trap nets (all ports)	24	0.2	1.1

[a] Unweighted mean of differences for individual pairings; in each individual comparison the average age or weight of the sample falling in the second group was subtracted from that of the sample falling in the first group.

[b] As an example, in 1943 (Table VI) the port of Erie is "easterly" and Vermillon is "westerly" (gill nets), and the port of Conneaut is "easterly" and Lorain "westerly" for trap nets.

A detailed comparison of year-class composition in fall and the following spring is not possible because only two spring collections are available. The relation between the year-class composition of the collections in the spring and the preceding fall was not the same in the two pairs of samples (Table VIII).

The agreement between the spring collection at Wheatley in 1952 and the collection of the preceding fall at Conneaut (no sample from Wheatley in the fall of 1951) was reasonably good. The dominant 1945 year-class contributed 34.5% of the total in both seasons and the difference of only 0.3 year in mean age (5.6 growing seasons in the fall and 5.3 in the spring) was inconsequential. On the other hand, the year-class compositions of blue pike collected at Conneaut in April 1951 and in October 1950 did not agree equally well. The fall collection was dominated by the 1945 year-class (44.8% but dominance shifted to the 1946 year-class (36.0%) in the April 1951 sample. The difference in mean age (5.8 growing seasons in the fall, 5.1 in the spring) was more than twice the difference between the mean ages of fish collected in the fall of 1951 and in the spring of 1952.

The evidence from the two comparisons throws doubt on the usefulness of data on year-class composition of fall samples for the analysis of statistics for the spring fishery. Despite the probability that factors or events that affected the fall fishery also affected the spring fishery, sampling errors in the fall would be greatly magnified if applied to the high production period in the spring; consequently, the description of the year-class contributions that follows is restricted to the fall fishery.

AGE AND YEAR-CLASS COMPOSITION

The age composition of blue pike in the 1943–59 samples varied widely from year to year (Table VI, Fig. 4). Samples were dominated by age-group

TABLE VIII. Year-class compositions (expressed as percentages) of blue pike taken in the spring and fall, 1950–52.

Seasons compared and ports of capture	Date of collection	No. of fish	Year-class										Average age[a]
			1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	
Fall 1951; spring 1952													
Conneaut	October 4, 1951	214	–	–	–	4.3	21.0	34.5	21.5	9.8	8.9	–	5.6
Wheatley	April 2, 1952	122	–	–	–	1.6	17.2	34.5	18.8	10.7	17.2	–	5.3
Fall 1950; spring 1951													
Conneaut	October 19, 1950	136	–	–	–	–	21.3	44.8	27.9	3.0	1.5	1.5	5.8
Conneaut	April 23, 1951	353	0.3	–	0.3	0.8	7.1	26.6	36.0	24.4	3.4	1.1	5.1

[a] Number of growing seasons.

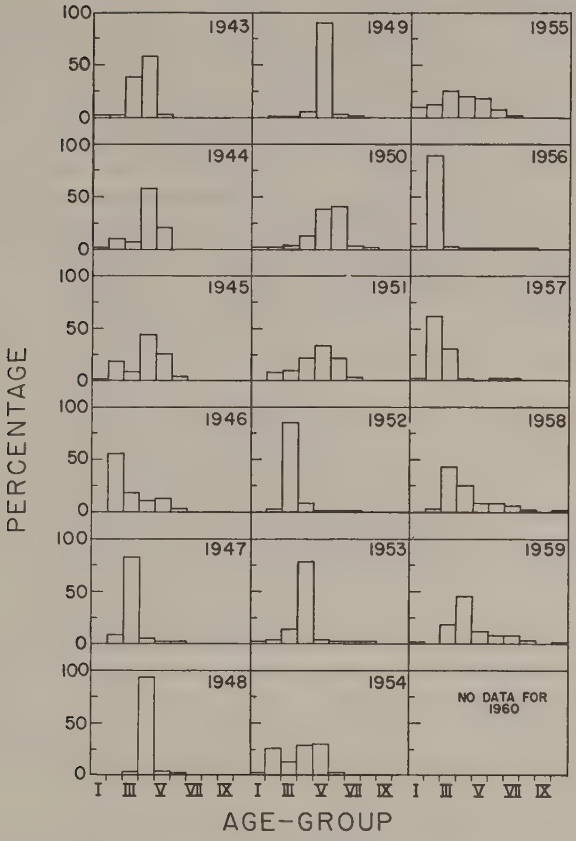

FIG. 4. Age compositions (expressed in percentages of total numbers) of samples of blue pike, 1943–59.

IV in 6 of the 17 years, by age-group III in 4 years, II in 3, V in 3, and VI in 1 year. Dominance or unusual strength of age-groups usually was attributable to the strength of particular year-classes.

The successive dominance of age-groups II though VI in 1946–50 demonstrates the overwhelming effect of the 1944 year-class on the age composition of the blue pike over this period (Table VI). The 1949 year-class had a similar, though less pronounced, effect on age composition in 1952–54. The only other year-class that dominated the fishery more than 1 year was the weak 1955 year-class, which appeared during the collapse of the fishery.

Age-groups VII and older appeared to be relatively stronger in the catches after 1954, probably due to declining numbers of younger fish and increased fishing with large-mesh gill nets rather than to an increase in actual abundance of older fish.

LENGTHS AND WEIGHTS

Length distributions and modes of the samples of blue pike (Table IX) exhibit clearly an increase of modal lengths within each of the periods 1943–45, 1946–50, 1951–55, and 1956–59. These periods of increase appear to have been closely related to the increases in length of dominant year-classes as they passed through the fishery. For example, during 1946–50, when the 1944 year-class dominated the samples, average lengths of this year-class increased progressively from 11.5 inches to 13.4 inches (Table X), and the mode of all fish in the samples increased from 11.0–11.4 to 13.5–13.9 inches (Table IX). The strong 1939 and 1940 year-classes were largely responsible for the increases in modal lengths from 1943 to 1945, as were the 1949 year-class from 1952 to 1954 and the fast growing 1954 and 1955 year-classes from 1956 to 1959.

Despite the effect of dominant year-classes on short-term trends in length distribution, mean lengths of blue pike in the fishery varied little from 1943 to 1954 (Table X). The average lengths of fish in samples fell within the limited range of 11.8–13.1 inches and fluctuations of average lengths of the different age-groups showed no distinct trends. For example, average lengths of fish of age-group III fluctuated only between 11.0 and 12.7 inches during the 12 years.

The average length of blue pike in the samples, and in each age-group and year-class, increased substantially after 1954 except in 1956. The average length changed from 14.4 in 1955 to 19.8 in 1959. The decrease from 14.4 inches in 1955 to 12.8 in 1956 was due to the strong representation of young fish (age-group II) in the fishery (average age dropped from 3.5 years in 1955 to 2.1 in 1956).

The increase in average length of fish of an age-group in successive years is best demonstrated by age-group IV: average lengths from 1954 to 1959 were 12.5, 14.8, 16.4, 17.7, 18.4, and 18.9 inches. Other well-represented age-groups (except II and III in 1956) showed similar increases in length.

Since the 1954 and 1955 year-classes contributed 78% of the catches from 1956 to 1959, these two year-classes describe generally the increase in both length and growth rate of blue pike after 1954. Average lengths of the 1954 year-class as age-groups I to V, from 1955 to 1959, were 11.6, 12.6, 15.3, 18.4, and 20.4 inches (annual increments 1.0, 2.7, 3.1, and 2.0 inches). Average lengths of the 1955 year-class as age-groups I to IV, from 1956 to 1959, were 11.8, 14.5, 17.8, and 18.9 inches (annual increments, 2.7, 3.3, and 1.1 inches).

The average weights of blue pike of each age-group in the annual collections also show the increase in growth rate and size after 1954 (Table XI). In 1943–54 the average weights of fish (age-groups combined) in the collections ranged from 7.7 oz to 11.0 oz, but in 1955–59 the range of the means was 11.7 to 60.5 oz. The average weight was lowest in 1952 and highest in 1959. Average weights of the individual age-groups (I to VIII) ranged from 5.0 to 13.1 oz in 1950 and from 23.0 to 114.3 oz in 1959. Blue pike of age-group III were almost eight times heavier in 1959 than in 1951.

TABLE IX. Percentage length distributions of blue pike in samples from the commercial fishery of Lake Erie, 1943–59. (Asterisks indicate modes.)

Length (*inches*)	Year of collection																
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
7.5– 7.9	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	–	–	–
8.5– 8.9	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–
9.0– 9.4	–	–	–	–	–	–	–	0.2	0.9	–	0.5	–	–	–	–	–	–
9.5– 9.9	–	–	1.4	–	0.6	–	–	0.5	0.9	0.1	2.8	–	–	0.1	–	–	–
10.0–10.4	0.6	0.6	1.4	1.2	4.8	2.0	1.7	0.2	5.6	4.1	4.6	–	–	0.2	–	–	–
10.5–10.9	2.9	1.8	5.8	6.1	14.5	9.1	4.4	2.0	8.9	13.4	6.8	0.5	0.8	2.3	–	–	–
11.0–11.4	10.3	2.2	5.8	20.1*	18.0*	20.3	15.0	4.5	20.5*	20.7	11.0	3.6	3.9	4.4	–	–	–
11.5–11.9	17.7	8.6	7.6	16.7	14.4	32.6*	22.1	6.7	17.7	23.7*	16.1	11.4	8.0	14.3	0.5	–	–
12.0–12.4	25.0*	18.6	6.9	10.2	12.3	22.9	25.0*	12.2	11.7	16.1	18.5*	15.6	3.2	20.7	1.8	–	–
12.5–12.9	21.3	25.9*	14.2	4.7	11.9	8.6	17.8	13.0	11.7	12.1	12.5	15.6	5.1	22.7*	2.2	–	–
13.0–13.5	11.4	22.0	20.2*	8.5	9.9	2.5	7.8	18.4	7.5	5.6	13.4	28.6*	6.2	18.8	6.4	–	–
13.5–13.9	5.1	11.9	17.5	8.2	6.5	1.0	3.9	19.6*	5.1	2.8	5.7	14.7	7.9	7.4	11.9	–	–
14.0–14.4	4.8	7.2	11.1	6.0	4.0	1.0	1.7	13.6	2.3	0.9	3.8	6.7	10.9	3.1	21.9*	–	–
14.5–14.9	0.4	1.2	5.6	4.0	2.2	–	0.6	6.6	1.9	0.1	1.7	1.7	11.4*	0.7	14.4	1.8	–
15.0–15.4	0.3	–	2.2	8.1	0.9	–	–	2.1	1.4	–	1.2	0.3	9.3	1.0	13.0	1.8	1.2
15.5–15.0	0.2	–	0.3	3.0	–	–	–	0.2	0.5	–	0.2	0.3	7.1	0.9	8.5	2.8	–
16.0–16.4	–	–	–	1.6	–	–	–	–	0.5	0.2	0.2	1.0	8.1	1.1	6.6	0.9	1.2
16.5–16.9	–	–	–	1.4	–	–	–	0.2	0.5	–	0.2	–	4.8	1.1	2.2	8.3	–
17.0–17.4	–	–	–	0.2	–	–	–	–	0.5	–	–	–	5.2	0.1	3.2	9.1	5.0
17.5–17.9	–	–	–	–	–	–	–	–	0.9	0.1	0.2	–	4.0	0.4	2.5	11.9	5.0
18.0–18.4	–	–	–	–	–	–	–	–	–	–	–	–	1.7	0.4	2.6	19.3*	7.5
18.5–18.9	–	–	–	–	–	–	–	–	0.5	–	0.3	–	0.6	–	–	16.5	15.0*
19.0–19.4	–	–	–	–	–	–	–	–	–	–	–	–	0.8	0.3	1.4	7.3	13.8
19.5–19.9	–	–	–	–	–	–	–	–	0·5	–	–	–	0.3	–	0.9	5.5	3.8
20.0–20.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	8.8
20.5–20.9	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–	3.7	7.5
21.0–21.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	5.0
21.5–21.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	3.8
22.0–22.4	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	2.8	5.0
22.5–22.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	1.2
23.0–23.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4
23.5–23.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
24.0–24.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
24.5–24.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
25.0–25.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4
26.0–26.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–
No. of fish	705	264	400	338	798	913	521	393	214	648	708	443	666	1066	240	109	108
Mean length	12.2	12.8	12.9	12.3	12.1	12.4	12.4	13.1	11.9	11.8	12.2	12.7	14.4	12.8	15.0	18.5	19.8

TABLE X. Average total lengths (inches) of blue pike for different age-groups and years of collection, Lake Erie, 1943–59. (Numbers of fish in parentheses.)

	Age-group[a]									
Year	I	II	III	IV	V	VI	VII	VIII	X	Average
1943	11.2	11.8	11.9	12.3	13.8	–	–	–	–	12.2
	(1)	(11)	(268)	(413)	(12)	–	–	–	–	(705)
1944	10.9	12.2	12.6	12.9	13.1	–	–	–	–	12.8
	(2)	(27)	(20)	(155)	(60)	–	–	–	–	(264)
1945	11.5	11.2	12.2	13.3	13.6	13.9	–	–	–	12.9
	(1)	(74)	(31)	(173)	(104)	(17)	–	–	–	(400)
1946	–	11.5	12.3	13.8	14.4	14.8	–	–	–	12.3
	–	(191)	(58)	(38)	(40)	(11)	–	–	–	(338)
1947	–	11.0	12.0	13.6	14.4	16.0	–	–	–	12.1
	–	(77)	(656)	(46)	(15)	(4)	–	–	–	(798)
1948	–	–	11.6	12.4	12.5	13.0	–	16.6	–	12.4
	–	–	(35)	(853)	(22)	(2)	–	(1)	–	(913)
1949	–	11.9	11.1	11.9	12.4	13.0	12.2	–	–	12.4
	–	(3)	(2)	(30)	(469)	(15)	(2)	–	–	(521)
1950	10.2	11.4	12.2	12.7	13.1	13.4	13.7	14.2	–	13.1
	(4)	(3)	(7)	(58)	(150)	(159)	(11)	(1)	–	(393)
1951	–	10.6	11.0	11.2	12.0	13.0	14.5	–	–	11.9
	–	(19)	(21)	(46)	(74)	(45)	(9)	–	–	(214)
1952	–	11.3	11.8	11.9	12.6	13.9	17.1	–	–	11.8
	–	(22)	(546)	(64)	(11)	(4)	(1)	–	–	(648)
1953	9.9	11.1	11.9	12.2	12.4	12.8	12.7	17.8	–	12.2
	(2)	(14)	(103)	(549)	(26)	(9)	(1)	(4)		(708)
1954	12.3	12.4	12.7	12.5	13.2	13.4	–	–	–	12.7
	(5)	(115)	(59)	(130)	(132)	(2)	–	–	–	(443)
1955	11.6	13.3	14.1	14.8	15.9	16.5	15.6	–	–	14.4
	(76)	(85)	(170	(139))	(134)	(60)	(2)	–	–	(666)
1956	11.8	12.6	13.0	16.4	16.8	16.7	16.8	17.8	–	12.8
	(34)	(970)	(14)	(6)	(10)	(15)	(16)	(1)	–	(1,066)
1957	12.4	14.5	15.3	17.7	18.0	18.7	17.7	18.2	–	15.0
	(4)	(147)	(73)	(4)	(2)	(5)	(2)	(3)	–	(240)
1958	–	15.0	17.8	18.4	20.0	19.2	19.9	24.0	18.4	18.5
	–	(4)	(46)	(28)	(10)	(10)	(8)	(2)	(1)	(109)
1959	15.0	–	18.7	18.9	20.4	20.6	23.1	23.7	24.7	19.8
	(1)	–	(21)	(50)	(11)	(10)	(10)	(4)	(1)	(108)

[a] Fish in these fall collections had completed or nearly completed the growing season in the year of capture (e.g. fish in age-group I had completed two growing seasons). Age-group IX was not represented in the collections.

The average weights of blue pike of the strong year-classes of 1944, 1949, and 1954 in successive annual samples further demonstrate the increased growth rate of fish of all ages after 1954 (Fig. 5). The 1944 year-class grew slowly; average weights were 6.5 oz as age-group I (1 fish) and 14.4 oz at age-group VII; annual increments were 0.1 to 3.1 oz. The average weight of fish of the

TABLE XI. Average weights (ounces) of blue pike in different age-groups and years of collection, Lake Erie, 1943–59. (Numbers of fish in parentheses.)

	Age-group[a]									
Year	I	II	III	IV	V	VI	VII	VIII	X	Average
1943	7.0	8.2	8.6	9.5	13.8	–	–	–	–	9.2
	(1)	(11)	(268)	(413)	(12)	–	–	–	–	(705)
1944	5.4	9.2	10.7	11.1	11.5	–	–	–	–	11.0
	(2)	(27)	(20)	(155)	(60)	–	–	–	–	(264)
1945	6.5	6.0	8.2	10.6	11.7	12.8	–	–	–	9.9
	(1)	(74)	(31)	(173)	(104)	(17)	–	–	–	(400)
1946	–	6.6	8.2	11.8	13.6	14.3	–	–	–	8.5
	–	(191)	(58)	(38)	(40)	(11)	–	–	–	(338)
1947	–	5.9	7.8	11.3	14.1	15.5	–	–	–	8.0
	–	(77)	(656)	(46)	(15)	(4)	–	–	–	(798)
1948	–	–	7.9	9.4	9.8	10.1	–	22.8	–	9.4
	–	–	(35)	(853)	(22)	(2)	–	(1)	–	(913)
1949	–	7.8	6.0	8.0	9.5	10.6	9.1	–	–	9.5
	–	(3)	(2)	(30)	(469)	(15)	(2)	–	–	(521)
1950	5.0	6.3	8.2	9.2	10.3	11.3	12.2	13.1	–	10.5
	(4)	(3)	(7)	(58)	(150)	(159)	(11)	(1)	–	(393)
1951	–	5.0	5.9	6.2	7.9	10.4	14.4	–	–	7.9
	–	(19)	(21)	(46)	(74)	(45)	(9)	–	–	(214)
1952	–	7.0	7.5	8.0	8.5	18.1	32.0	–	–	7.7
	–	(22)	(546)	(64)	(11)	(4)	(1)	–	–	(648)
1953	1.8	6.7	7.3	8.4	9.0	11.5	11.4	28.8	–	8.3
	(2)	(14)	(103)	(549)	(26)	(9)	(1)	(4)	–	(708)
1954	9.4	9.2	10.5	10,7	12.2	12.3	–	–	–	10.7
	(5)	(115)	(59)	(130)	(132)	(2)	–	–	–	(443)
1955	7.8	12.7	16.2	19.1	24.8	27.9	22.2	–	–	18.2
	(76)	(85)	(170)	(139)	(134)	(60)	(2)	–	–	(666)
1956	8.5	10.9	12.2	26.3	32.7	27.7	31.8	36.0	–	11.7
	(34)	(970)	(14)	(6)	(10)	(15)	(16)	(1)	–	(1,066)
1957	10.8	18.4	23.2	34.5	43.8	46.7	39.8	35.7	–	21.1
	(4)	(147)	(73)	(4)	(2)	(5)	(2)	(3)		(240)
1958	–	19.5	38.1	41.9	62.1	52.6	56.1	103.0	40.0	44.5
	–	(4)	(46)	(28)	(10)	(10)	(8)	(2)	(1)	(109)
1959	23.0	–	46.5	49.4	68.8	72.5	99.2	114.3	128.8	60.5
	(1)	–	(21)	(50)	(11)	(10)	(10)	(4)	(1)	(108)

[a]Fish in these fall collections had completed or nearly completed the growing season in the year of capture (e.g. fish in age-group I had completed two growing seasons). Age-group IX was not represented in the collections.

1949 year-class was 5.0 oz as age-group I and 12.2 oz as age-group V, but then increased to 31.8 oz as age-group VII in 1956. Weight of fish of the 1954 year-class increased from 7.8 oz in 1955 (age-group I) to 68.8 oz in 1959 (age-group V); successive annual increments in ounces were 3.1, 12.3, 18.7, and 26.9.

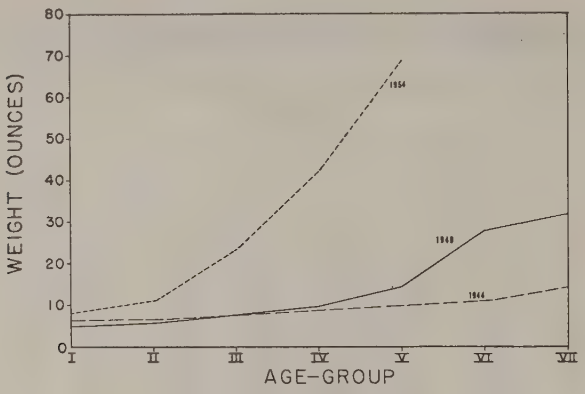

FIG. 5. Average weights (ounces) of blue pike of the year-classes 1944 (long dashes), 1949 (solid line), and 1954 (short dashes) at different ages.

Average weights of age-groups III, IV, and V in successive annual samples also demonstrate the changes in the size of fish in the fishery (Fig. 6). The greatest increases in weight, which occurred after 1956, were coincident with the sharp decline in commercial production.

CONTRIBUTIONS OF YEAR-CLASSES

Contributions of year-classes to the fall production of blue pike were estimated for year-classes that contributed all or most of their production

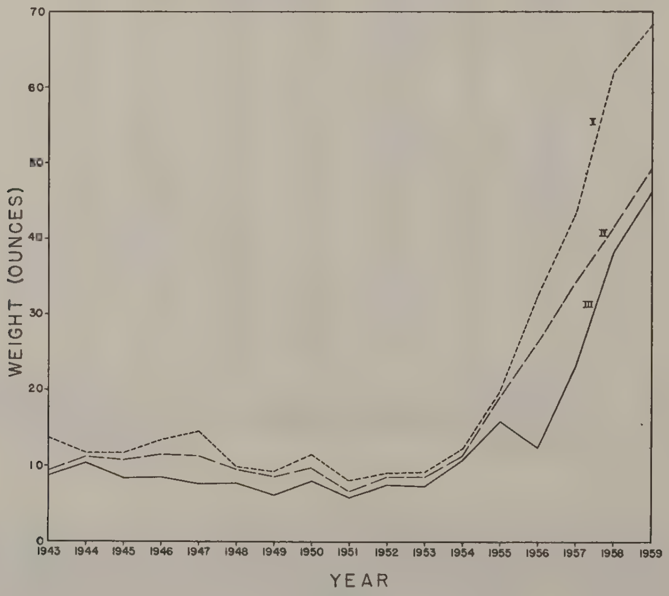

FIG. 6. Average weights of age-group III (solid line), age-group IV (long dashes), and age-group V (short dashes) of blue pike samples from the fall commercial landings of Lake Erie, 1943–59.

from 1941 to 1959. Of the 20 year-classes represented in the 1943–59 samples, contributions were estimated for the 18 consecutive year-classes 1939–56. Omitted from the estimated contributions were the 1938 year-class, which appeared only in the 1943 samples, and the 1958 year-class, which constituted less than 1% of the 1959 sample.

Contributions of year-classes were estimated by both number and weight. The percentages by number and weight of each age-group in the annual samples (from Table VI) were applied directly to the total fall catch for the year of each sample.

Since production was not recorded by season for the entire lake, estimates of fall production each year in Pennsylvania, New York, and Ontario and for some years in Ohio were based on the percentage production in the fall fishery (September–December) in Ohio in 1948–59 (Table XII). The average

TABLE XII. Spring and fall production (thousands of pounds) of blue pike in Ohio waters and estimated spring and fall production for all waters in Lake Erie, 1948–59. (Percentages given in parentheses.)

	Production in Ohio waters			Production in all waters (estimated)		
Year	Spring[a]	Fall	Total	Spring	Fall	Total
1948	3,131 (45)	3,826 (55)	6,957	6,635	8,110	14,745
1949	7,962 (75)	2,654 (25)	10,616	17,837	5,946	23,783
1950	4,116 (84)	784 (16)	4,900	12,433	2,368	14,801
1951	1,419 (76)	448 (24)	1,867	4,609	1,455	6,064
1952	885 (16)	4,646 (84)	5,531	2,249	11,789	14,038
1953	4,934 (72)	1,919 (28)	6,853	13,320	5,145	18,375
1954	2,974 (65)	1,602 (35)	4,576	9,358	5,038	14,396
1955	2,869 (78)	810 (22)	3,679	15,354	4,331	19,685
1956	2,916 (62)	1,787 (38)	4,703	11,691	7,166	18,857
1957	2,653 (91)	262 (9)	2,915	9,437	933	10,370
1958	362 (99)	4 (1)	366	1,245	154	1,339
1959	19 (94)	1 (6)	20	75	4	79

[a] For purposes of licensing and reporting, the "spring" fishing season in Ohio is from March 15 to August 31 and the "fall" season is from September 1 to December 20.

percentage of the annual production landed in the fall in Ohio from 1948 to 1956 (36%) was used to estimate fall production in all years in Ontario, New York, and Pennsylvania, and in Ohio in 1941–47.

The weight contributions of age-groups II and III of the 1939 year-class in 1941 and 1942 and age-group II of the 1940 year-class in 1942 were estimated to complete the record of the total contributions of these year-classes to the fishery. The estimates were based on long-term (1943–54) ratios of catches among age-groups II to VI. These ratios were computed by dividing the estimated production of each of age-groups II to VI separately into the estimated production of each younger age-group. Ratios of production for each age-group were: age-group II was 0.18 of age-group III, 0.09 of age-group IV, 0.07 of age-group V, and 0.13 of age-group VI; and age-group III was 0.46 of age-group IV, 0.39 of age-group V, and 0.70 of age-group VI. As an example, the estimate of the pounds of fish produced in 1941 by age-group II of the 1939 year-class was determined by multiplying its estimated production in 1942 (as age-group III) by 0.18, in 1943 (as age-group IV) by 0.09, in 1944 (as age-group V) by 0.07, and in 1945 (as age-group VI) by 0.13, and then averaging the products.

The numbers of fish of the 1939 and 1940 year-classes produced in 1941–42 were estimated by dividing the number of fish per pound (based on the average weights of fish in each of the age-groups II and III in the samples collected in 1943–54) into the estimated poundage for each age-group.

The estimated contributions of only 5 of the 18 year-classes (1939, 1940, 1944, 1949, 1954) in the fishery exceeded the 1941–59 mean (Table XIII). The 1944 and 1949 year-classes dominated the catch and the two combined contributed 46.4% by number and 41.6% by weight (Table XIV) of the total 1941–59 fall catch from the 1939–56 year-classes. Fish of one or both of the 1944 and 1949 year-classes were present in the fishery from 1945 to 1959. The extent to which the 1944 and 1949 year-classes dominated the fall fishery during these years is demonstrated graphically in Fig. 7. The 1944 year-class contributed 28,155,000 fish (21.9% of the 1941–59 total and 394.7% of the 1941–59 mean contribution of year-classes 1939–56) or 16,083,000 lb (371.0% of the mean for all year-classes). The 1949 year-class contributed 31,407,000 fish (24.5% of the total and 440.3% of the mean of year-classes) or 16,385,000 lb (378.2% of the mean of year-classes).

Less important contributions were made by year-classes 1939 (11,995,000 fish, 9.3% of the total), 1940 (14,641,000 fish, 11.4%), and 1954 (9,597,000 fish, 7.5%); their combined contribution to the total was 28.2%. The other 13 year-classes together contributed only 25.3% of the fish produced by the 1939–56 year-classes. No fish of the 1957 year-class and only one fish of the 1958 year-class were collected, even though fish of both year-classes should have been well above commercial length by the fall of 1959.

Slightly greater percentage contributions by weight than by numbers were made by the 1950–56 year-classes, which were in the fishery after 1954,

Table XIII. Numbers (thousands) of fish and percentages of the total numbers contributed by different year-classes of blue pike to the fall fishery of Lake Erie, 1941–59.[a]

Year-class	Year of capture																			Total for year-class		
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	No. of fish	Percentage of 1941–59 total	Percentage of 1941–59 mean
1939																						
Age	II	III	IV	V	VI	–	–		–	–	–	–	–	–	–	–	–	–	–			
Number	287	1,522	6,955	2,882	349	–	–	–	–	–	–	–	–	–	–	–		–	–	11,995	9.3	168.2
Percentage	10.1	23.4	58.6	22.7	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
1940																						
Age	–	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–			
Number	–	412	4,510	7,452	2,160	107	–	–	–	–	–	–	–	–	–	–	–	–	–	14,641	11.4	205.3
Percentage	–	6.3	38.0	58.7	26.0	3.2	–	–	–	–	–	–	–	–	–	–	–	–	–			
1941																						
Age	–	–	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–	–	–			
Number	–	–	190	965	3,596	393	17	14	–	–	–	–	–	–	–	–	–	–	–	5,175	4.0	72.5
Percentage	–	–	1.6	7.6	43.3	11.8	0.5	0.1	–	–	–	–	–	–	–	–	–	–	–			
1942																						
Age	–	–	I	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–	–	–	–			
Number	–	–	12	1,295	641	376	65	28	40	11	–	–	–	–	–	–	–	–	–	2,468	1.9	34.6
Percentage	–	–	0.1	10.2	7.7	11.3	1.9	0.2	0.4	0.3	–	–	–	–	–	–	–	–	–			
1943																						
Age	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–			
Number	–	–	–	102	1,538	590	196	330	290	101	–	–	–	–	–	–	–	–	–	3,147	2.5	44.1
Percentage	–	–	–	0.8	18.5	17.7	5.7	2.4	2.9	2.8	–	–	–	–	–	–	–	–	–			
1944																						
Age	–	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–			
Number	–	–	–	–	25	1,865	2,821	12,873	8,990	1,453	128	–	–	–	–	–	–	–	–	28,155	21.9	394.7
Percentage	–	–	–	–	0.3	56.0	82.2	93.5	90.0	40.4	4.3	–	–	–	–	–	–	–	–			
1945																						
Age	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–			
Number	–	–	–	–	–	–	333	523	569	1,375	627	24	60	–	–	–	–	–	–	3,511	2.7	49.2
Percentage	–	–	–	–	–	–	9.7	3.8	5.7	38.2	21.0	0.1	0.6	–	–	–	–	–	–			
1946																						
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	VII	–	–	–	–	–	–			
Number	–	–	–	–	–	–	–	–	40	529	1,030	147	10	–	–	–	–	–	–	1,756	1.4	24.6
Percentage	–	–	–	–	–	–	–	–	0.4	14.7	34.5	0.6	0.1	–	–	–	–	–	–			
1947																						
Age	–	–	–	–	–	–	–	–	II	III	IV	V	VI	–	–	–	–	–	–			
Number	–	–	–	–	–	–	–	–	60	65	641	441	89	–	–	–	–	–	–	1,296	1.0	18.2
Percentage	–	–	–	–	–	–	–	–	0.6	1.8	21.5	1.8	0.9	–	–	–	–	–	–			
1948																						
Age	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	X	–			
Number	–	–	–	–	–	–	–	–	–	29	292	2,428	377	38	11	10	–	–	–	3,185	2.5	44.6
Percentage	–	–	–	–	–	–	–	–	–	0.8	9.8	9.9	3.8	0.5	0.3	0.1	–	0.9	–			

(Continued)

TABLE XIII. Numbers (thousands) of fish and percentages of the total numbers contributed by different year-classes of blue pike to the fall fishery of Lake Erie, 1941–59.[a] (*Concluded*)

Year-class	Year of capture																			Total for year-class		
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	No. of fish	Percentage of 1941–59 Total	Percentage of 1941–59 mean
1949																						
Age	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII	VIII	–	X			
Number	–	–	–	–	–	–	–	–	–	36	265	20,647	7,714	2,252	347	137	9	–	–	31,407	24.5	440.3
Percentage	–	–	–	–	–	–	–	–	–	1.0	8.9	84.2	77.7	29.8	9.1	1.4	1.3	–	0.9			
1950																						
Age	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–			
Number	–	–	–	–	–	–	–	–	–	–	–	834	1,450	2,214	766	137	6	1	–	5,408	4.2	75.8
Percentage	–	–	–	–	–	–	–	–	–	–	–	3.4	14.6	29.3	20.1	1.4	0.8	1.8	–			
1951																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII			
Number	–	–	–	–	–	–	–	–	–	–	–	–	200	1,005	797	69	15	4	–	2,090	1.6	29.3
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	2.0	13.3	20.9	0.7	2.1	7.3	3.7			
1952																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII			
Number	–	–	–	–	–	–	–	–	–	–	–	–	30	1,965	972	88	6	5	–	3,066	2.4	43.0
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	0.3	26.0	25.5	0.9	0.8	9.2	9.3			
1953																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	83	484	128	12	5	–	712	0.6	10.0
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	12.7	1.3	1.7	9.2	9.3			
1954																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	434	8,934	215	14	–	9,597	7.5	134.5
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.4	91.0	30.4	25.7	10.2			
1955																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	314	434	24	1	773	0.6	10.8
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.2	61.2	42.2	46.3			
1956																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	2	–	14	–	–
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7	3.7	19.4			
Total	287	1,934	11,667	12,696	8,309	3,331	3,432	13,768	9,989	3,599	2,983	24,521	9,930	7,557	3,811	9,817	709	55	1	128,396		

[a] Year-class contributions of less than 500 fish and percentages less than 0.05 are not recorded.

[b] Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year it appeared in the samples, estimated contributions in 1941 to 1943 are less than the local production in those years and percentages do not equal 100; age-group I (1 fish, 0.9 %) in 1959 omitted.

TABLE XIV. Estimated contributions (thousands of pounds) of different year-classes of blue pike to the fall fishery of Lake Erie 1941–59.[a]

Year-class	Year of capture																			Total for year-class		
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	Pounds	Percentage of 1941–59 total	Percentage of 1941–59 mean
1939																						
Age	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Pounds	183	973	4,189	2,075	263	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7,679	9.8	177.2
Percentage	10.5	25.4	60.0	23.7	5.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
1940																						
Age	–	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–			
Pounds	–	261	2,534	5,175	1,558	96	–	–	–	–	–	–	–	–	–	–	–	–	–	9,624	12.3	222.1
Percentage	–	6.8	36.3	59.1	30.2	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–			
1941																						
Age	–	–	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–	–	–			
Pounds	–	–	91	639	2,322	301	19	16	–	–	–	–	–	–	–	–	–	–	–	3,388	4.3	78.2
Percentage	–	–	1.3	7.3	45.0	17.0	1.1	0.2	–	–	–	–	–	–	–	–	–	–	–			
1942																						
Age	–	–	I	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–	–	–	–			
Pounds	–	–	7	832	356	227	58	16	24	7	–	–	–	–	–	–	–	–	–	1,527	2.0	35.2
Percentage	–	–	0.1	9.5	6.9	12.8	3.4	0.2	0.4	0.3	–	–	–	–	–	–	–	–	–			
1943																						
Age	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–			
Pounds	–	–	–	35	650	280	141	203	184	24	–	–	–	–	–	–	–	–	–	1,517	1.9	35.0
Percentage	–	–	–	0.4	12.6	15.8	8.2	2.5	3.1	1.0	–	–	–	–	–	–	–	–	–			
1944																						
Age	–	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–			
Pounds	–	–	–	–	10	868	1,332	7,615	5,393	753	112	–	–	–	–	–	–	–	–	16,083	20.6	371.0
Percentage	–	–	–	–	0.2	49.0	77.6	93.9	90.7	31.8	7.7	–	–	–	–	–	–	–	–			
1945																						
Age	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–			
Pounds	–	–	–	–	–	–	166	260	309	822	406	83	113	–	–	–	–	–	–	2,159	2.8	49.8
Percentage	–	–	–	–	–	–	9.7	3.2	5.2	34.7	27.9	0.7	2.2	–	–	–	–	–	–			
1946																						
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	VII	–	–	–	–	–	–			
Pounds	–	–	–	–	–	–	–	–	12	648	506	165	–	–	–	–	–	–	–	1,331	1.7	30.7
Percentage	–	–	–	–	–	–	–	–	0.2	27.4	34.7	1.4	0.2	–	–	–	–	–	–			
1947																						
Age	–	–	–	–	–	–	–	–	II	III	IV	V	VI	–	–	–	–	–	–			
Pounds	–	–	–	–	–	–	–	–	24	78	244	248	87	–	–	–	–	–	–	681	0.9	15.7
Percentage	–	–	–	–	–	–	–	–	0.4	3.3	16.8	21.	1.7	–	–	–	–	–	–			
1948																						
Age	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	X	–			
Pounds	–	–	–	–	–	–	–	–	–	24	106	1,179	206	25	13	21	–	1	–	1,575	2.0	36.4
Percentage	–	–	–	–	–	–	–	–	–	1.0	7.3	10.0	4.0	0.5	0.3	0.3	–	0.8	–			

(Continued)

TABLE XIV. Estimated contributions (thousands of pounds) of different year-classes of blue pike to the fall fishery of Lake Erie 1941–59.[a] — (*Concluded*)

	Year of capture																			Total for year-class		
Year-class	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	Pounds	Percent-age of 1941–59 total	Percent-age of 1941–59 mean
1949																						
Age	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII	VIII	–	X			
Pounds	–	–	–	–	–	–	–	–	–	12	81	9,737	3,962	1,708	585	279	21	–	–	16,385	21.0	378.2
Percentage	–	–	–	–	–	–	–	–	–	0.5	5.6	82.6	76.9	33.9	13.5	3.9	2.3	–	2.0			
1950																						
Age	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–			
Pounds	–	–	–	–	–	–	–	–	–	–	–	377	689	1,476	1,182	222	14	7	–	3,967	5.1	91.6
Percentage	–	–	–	–	–	–	–	–	–	–	–	3.2	13.3	29.3	27.3	3.1	1.5	4.5	–			
1951																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	82	660	961	115	48	14	–	1,880	2.4	43.4
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	1.6	13.1	22.2	1.6	5.1	9.3	7.0			
1952																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	6	1,119	987	158	19	17	1	2,307	3.0	53.2
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	0.1	22.2	22.8	2.2	2.0	10.8	15.2			
1953																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	50	390	100	27	20	–	587	0.7	13.5
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	1.0	9.0	1.4	2.9	12.8	11.1			
1954																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	213	6,098	304	37	–	6,653	8.5	153.6
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.9	85.1	32.7	24.1	11.6			
1955																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	173	491	56	2	722	0.9	16.7
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4	52.6	36.1	37.8			
1956																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	2	1	11	–	–
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	1.6	14.9			
Total	183	1,234	6,281	8,756	5,159	1,772	1,716	8,110	5,946	2,368	1,455	11,789	5,145	5,038	4,331	7,166	933	154	4	78,076		

[a] Year-class contributions less than 500 pounds and percentages less than 0.05 are not recorded.

[b] Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year it appeared in the samples, estimated contributions in 1941 and 1943 are less than the total production in those years and percentages do not equal 100; age-group I (1 fish, 0.4% of the weight) in 1959 omitted.

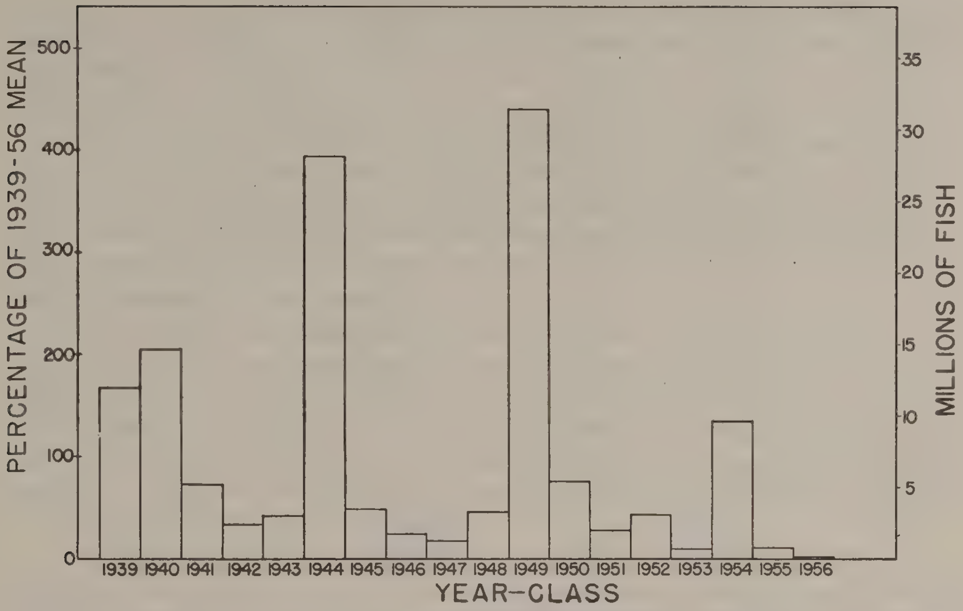

FIG. 7. Contributions of various year-classes of blue pike to the fall fishery of Lake Erie in 1941–59, expressed as total numbers and as percentage of the mean for year-classes 1939 to 1956.

when the marked improvement in growth rate increased the weight of fish in the various age-groups.

That fast growth was responsible in the later years for more rapid removal of young fish by the fishery is best shown by year-classes 1954–56. The contribution of these year-classes to the fishery was during the period of accelerated growth in 1955 and later years. Both year-classes were most abundant as age-groups I and II and few were older than age-group III.

EFFECT OF CHANGES IN ABUNDANCE ON THE FISHERY

Most of the stronger year-classes of blue pike contributed about half or more of their total yield (in pounds) to the fall fishery during a single season. These strong year-classes, the percentage of the total weight contribution of each during its peak season, and the age-group and year in which this percentage was taken were: 1939—54.6%, IV, 1943; 1940—53.8, IV, 1944; 1944—47.3, IV, 1948; 1949—59.4, III, 1952; and 1954—91.7, II, 1956. In numbers of fish, the total production for the peak fall season of each of these five year-classes amounted to 44.3% (56.9 million fish) of the total fall production (128.4 million) for the 18 year-classes in 1941–59.

The beginning or end of a period of heavy contribution of a year-class, as indicated by the Ohio trap-net fishery, sometimes was remarkably abrupt. The 1949 year-class, for example, yielded an average of 1028 fish per 10 trap-net lifts in the fall of 1952, as compared with 29 in the fall of 1951 (Table XV).

TABLE XV. Numbers of blue pike of different year-classes caught per 10 trap-net lifts in Ohio in the fall, 1948–56. (Catches less than 0.5 fish are excluded.)

Year	Year-class															
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
1948	1	2	20	813	38	–	–	–	–	–	–	–	–	–	–	–
1949	–	2	18	738	61	4	4	–	–	–	–	–	–	–	–	–
1950	–	1	5	95	91	36	5	2	6	–	–	–	–	–	–	–
1951	–	–	–	4	31	70	57	27	29	–	–	–	–	–	–	–
1952	–	–	–	–	1	4	20	116	1028	46	–	–	–	–	–	–
1953	–	–	–	–	–	–	4	26	562	101	19	5	–	–	–	–
1954	–	–	–	–	–	–	–	1	121	138	62	138	3	–	–	–
1955	–	–	–	–	–	–	–	1	14	30	42	63	40	56	–	–
1956	–	–	–	–	–	–	–	–	3	4	2	2	8	624	30	–
1957	–	–	–	–	–	–	–	–	1	–	1	–	1	18	43	2
1958	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1

Sharp declines in fall catch were shown by the 1944 year-class in 1950 (a drop from 738 to 95 per 10 trap-net lifts), the 1949 year-class in 1954, and the 1954 year-class in 1957.

The short periods of high abundance and the sudden disappearance of strong year-classes of blue pike from the fishery inflicted severe hardships on Lake Erie commercial fishermen. The purchase of gear, maintenance of vessels, and employment of fishermen were sometimes complex and frustrating because of the constantly changing catches. Fishermen not only were required to adjust fishing operations to sudden changes in abundance, but often were faced with glutted markets and low prices.

The average price per pound of blue pike landed from 1945 through 1958 was 22.2 cents and ranged from 11.1 to 27.2 cents. Significantly, changes in production of New York, Ohio, and Pennsylvania were related inversely ($r = -0.94$; $p = 0.001$; df $= 40$) to changes in average price per pound in these states during 1945–58. Since the market for blue pike was supplied almost entirely by fish from Lake Erie, prices of blue pike were controlled largely by the volume of production in that lake.

The collapse of the blue pike fishery forced most fishermen to seek lower priced species, such as yellow perch (*Perca flavescens*), white bass (*Roccus chrysops*), freshwater drum (*Aplodinotus grunniens*), and smelt (*Osmerus mordax*). Other fishermen were forced out of business.

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An Abnormally Colored C-O Sole, *Pleuronichthys coenosus*

A C-O sole which was albinistic and ambicolorate was taken during SCUBA diving in 30 feet of water near Alki Point (Seattle), Puget Sound, Washington, on October 3, 1965. The color of the fish on the eyed side was basically white with small to large irregular dark blotches (fig. 1). The blind side was white with a few dark to light-brown blotches on the body and especially on the fins (fig. 2).

No morphological anomalies were found in this abnormally colored fish. Eye placement and body form were normal. The number of rays of the dorsal (66) and anal (50) fins were within the range given by Clemens and Wilby (1961) and Fitch (1963). Total length was 20.4 cm.

The depth of capture of this anomalous C-O sole was not unusually shallow, since this species is seen frequently in depths of 6 to 12 feet in some areas of Puget Sound.

Fitch (1963) stated that ambicoloration in *Pleuronichthys* is rare except in *decurrens.* He mentioned that adult C-O sole often have dusky blotches on the blind side. It is assumed that albinistic conditions in the C-O sole are also rare. Possibly the dusky blotches on the blind side of the C-O sole described here are not as unusual as its partial albinism. Most significantly, this fish is both albinistic and ambicolorate.

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Fishery Biologist

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Figure 1. The right (top) side of an abnormally colored C-O sole showing the partial albinism. The wound was inflicted by collecting with a knife.

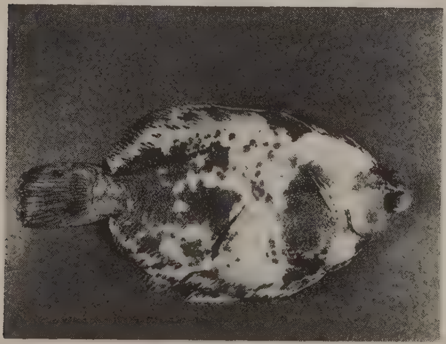
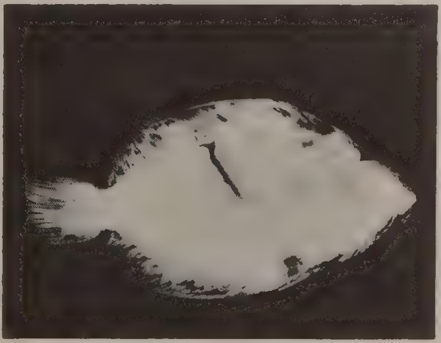


Figure 2. The left (bottom) side of the same fish showing partial ambicoloration.



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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

A NEW SPECIES AND TWO NEW SUBSPECIES OF SHRIMP OF THE GENUS *PENAEUS* FROM THE WESTERN ATLANTIC

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Many aspects of the biology of various species of *Penaeus* from Atlantic America, particularly of the three most common in North America, have been and continue to be the object of much research. Thus far, however, the information gleaned has little bearing on systematics, and only meager information has been accumulated in this field since Burkenroad (1934, 1939), published his major contributions to the systematics of the genus. He advanced considerably our understanding of the group, but the lack of adequate material prevented him from carrying his work to completion and often from reaching definite conclusions.

I have been able to assemble extensive collections from much of the range of the genus in the western Atlantic, and to carry out biometric studies. Such studies of large series of specimens have revealed several recognizable geographic taxa among the widely ranging species of *Penaeus*. Among them are the species and two subspecies described below. A monograph of the western Atlantic species, subspecies, and subpopulations, including full descriptions and figures, as well as an evaluation of the significant information on the biology of each, is near completion.

The present paper has been made possible through the cooperation of many institutions and individuals. I am particularly indebted to Fenner A. Chace and Horton H. Hobbs for many suggestions, to Daniel M. Cohen for continuous encouragement, and to Harvey R. Bullis for

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[1] Isabel C. Canet.

critical material from usually inaccessible localities. Also hearty thanks are due to María Manuela Diéguez de Farfante for preparing the drawings included here. The work was done with the support of the Radcliffe Institute for Independent Study, the Bureau of Commercial Fisheries, and the National Science Foundation (Grant No. GB-3907). The various institutions that made material available are cited by abbreviations before each lot to indicate where it is deposited: American Museum of Natural History (AMNH); Centro de Investigaciones Pesqueras, Cuba (CIP); Muséum National d'Histoire Naturelle, Paris (MNHNP); Museum of Comparative Zoölogy, Harvard University (MCZ); University of Miami Marine Laboratory (UMML); United States National Museum (USNM); and Peabody Museum of Natural History, Yale University (YPM).

Particularly useful information pertinent to the species and subspecies described below can be found in the following works: Boschi (1963), Burkenroad (1934, 1939), Davant (1963), Eldred and Hutton (1960), Holthuis (1959), Ives (1891), Lindner (1957), Magalhães (1944), Mistakidis (1965), Ortmann (1891), Pérez Farfante (1953, 1954), Pérez Farfante, Acosta, and Alemany (1961), da Silva (1965), Tremel and Mistakidis (1965).

Penaeus paulensis new species

Fig. 1 a–d

Camarão rosa, ("pink shrimp"); langostino

Penaeus brasiliensis: Ortmann, in part, 1891. Zool. Jahr. Abt. Syst. Geogr. Biol. 5(3): 445–449, table 36, Figs. 1 a–c; not *P. brasiliensis* Latreille 1817.

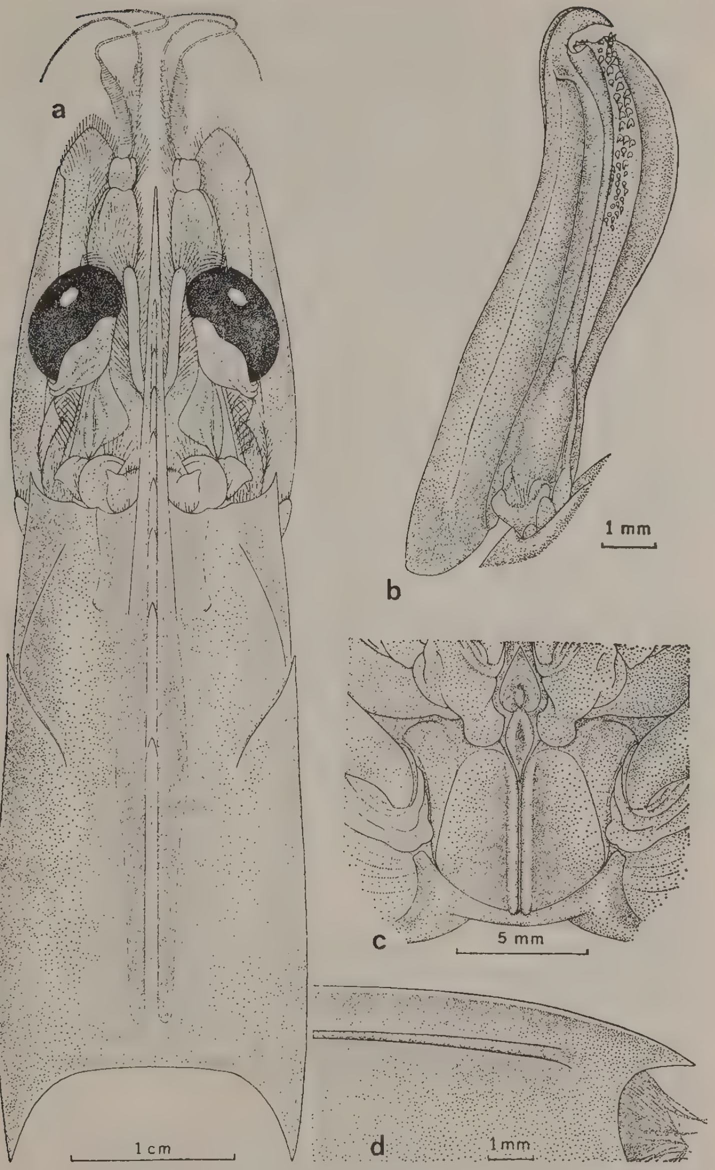
Penaeus aztecus: Burkenroad, in part ("Form C"), 1939. Bull. Bingham Oceanogr. Coll. 6, art. 6: 34–45, figs. 32, 33; not *P. aztecus* Ives 1891.

Holotype: 1♂, USNM 119128, Santos, São Paulo, Brazil, April 1964, M. Vannucci.

Paratypes: BRAZIL: Rio de Janeiro: 1♂, 1♀, MNHNP–USNM, off mouth Guanabara Bay, 34–65 fms, 2 December 1961, *Calypso* Sta. 105. 1♂, 1♀, YPM, Rio de Janeiro. 2♂, 2♀, USNM, Santana Island, 16 fms, SUDEPE. 1♀, USNM, off Rio de Janeiro, 23 August 1925, S. M. Waelsof. São Paulo: 3♂, 1♀, USNM, off São Sebastião, 20–35 fms, 10 December 1961, *Calypso* Sta. 129. 2♂, 2♀, MNHNP–USNM, off São Sebastião, 25–30 fms, 10 December 1961, *Calypso* Sta. 130. 3♂,

→

Fig. 1. *Penaeus paulensis* n. sp. *a,* Carapace, holotype ♂ 35 mm c.l., Santos, São Paulo, Brazil. *b,* Petasma, ♂ 39 mm c.l., S Point do Boi, São Paulo, Brazil. *c,* Thelycum, ♀ 49.5 mm c.l., Santos, São Paulo, Brazil. *d,* Sixth abdominal somite (posterodorsal portion), holotype.


a
b
1 mm
c
5 mm
d
1 cm
1 mm

MNHNP–USNM, São Sebastião, 11 fms, 11 December 1961, *Calypso* Sta. 135. 2♂, 1♀, MNHNP–USNM, off Point do Boi, 26–40 fms, 11 December 1961, *Calypso* Sta. 136. 12 ♂, 3♀, MNHNP–USNM, off Point do Boi, 36–30 fms, 11 December 1961, *Calypso* Sta. 137. 2♂, 3♀, USNM, Santos, 8 May 1964, M. Vannucci. 1♂, USNM, Santos, June 1913, H. Leuderwaldt. 1♂, USNM, Santos, 24 October 1949, Carvalho. 11♂, 11♀, USNM, Cananéia, September 1965, V. Sadowski. 4♂, 1♀, MNHNP–USNM, Laje dos Santos Island, 24–75 fms, 14 December 1961, *Calypso* Sta. 143. SANTA CATARINA: 4♂, 5♀, USNM, Lake da Conceição, Santa Catarina Island, 19 November 1965, E. Tremel. 3♂, 3♀, MNHNP–USNM, Zimbros Bay, 16 December 1961, *Calypso* Sta. 148. RIO GRANDE DO SUL: 1♀, MNHNP, off Mostardas, 17 December 1961, *Calypso* Sta. 151. 1♀, MNHNP, off Mostardas, 36–30 fms, 17 December 1961, *Calypso* Sta. 152. 9♂, 13♀, MCZ, Rio Grande, 7 June 1865?, G. Harrington. 3♂, 3♀, MNHNP–USNM, off southernmost end Rio Grande do Sul, 20 December 1961, *Calypso* Sta. 155. URUGUAY: 2♂, 3♀, USNM, Arroyo Balizas, Castillos Lake, 19 April 1961, H. Ferrando. 3♂, 1♀, USNM, Lake de Rocha, 18 April 1961, H. Ferrando. 2♂, 1♀, USNM, Lake de Rocha, 18 April 1961, H. Ferrando.

Description: Rostrum short, reaching at least distal half of second antennular segment but not beyond distal end of third, slender and straight in apical portion. Adrostral sulcus (Fig. 1a) broad along entire length, width 1 to 2 times postrostral carina width, long, ending $\frac{1}{12}$ to $\frac{1}{20}$ carapace length from posterior margin of carapace. Median sulcus short, ending well anterior to posterior end of adrostral sulcus; shallow, continuous or interrupted, often limited to anterior fossette.

Dorsolateral sulcus (Fig. 1 d) very narrow, relation between keel height and sulcus width (measured at distance about $\frac{1}{3}$ somite length from posterior margin) 3 to 15, modally 6. K/S (keel/sulcus) relation showing modal value of 6 for all size classes of both sexes.

Third pereopod short, reaching at least distal third of second but not beyond distal end of third antennular segment, shorter in larger individuals.

Petasma (Fig. 1 b): Ventral costa broad and blunt at distal end, extending proximally in extremely slight curve or almost straight line, with free distal border even or with faintly undulating flange; group of medium sized, irregularly set teeth close to apex. Membranous portion of ventrolateral lobule with band of spines, very narrow distally, moderately wide proximally. Distal fold of lateral lobe armed with prominent spinules.

Thelycum (Fig. 1 c): Apical process typically very narrow, bordered by nearly triangular or highly arched ridge, with knob often at center of slightly concave ventral surface. Posterior protuberance with median carina bifurcated anteriorly, forming two ridges converging at apical process, resulting in narrow, diamondshaped structure. Lateral plates with anteromedian angles divergent, leaving posterior protuberance exposed.

Color: Usually pinkish, thus the name camarão rosa ("pink shrimp") is applied to it in different localities within its range.

Size: The largest female examined was 54 mm c.l., 215 mm t.l., and the largest male, 40 mm c.l., 171 mm t.l.

Distribution: *P. paulensis* ranges from south of Cape Frio along the coast of Brazil to Lake de Rocha and, according to Burkenroad (1939), as far south as Montevideo, Uruguay. The specimen mentioned by Boschi (1963) in the Museo Bernardino Rivadavia, in Buenos Aires, labeled "North Patagonia," may possibly be a straggler from waters farther north.

Name: I have named this species for São Paulo State, Brazil, where it is fished commercially in large quantities offshore as well as in the estuarine waters along the coast.

Remarks: *P. paulensis* is closely allied to *P. aztecus aztecus* from northern waters and *Penaeus aztecus subtilis* (see below) from the Caribbean Sea and the Atlantic off northern–eastern South America. It differs from both by the narrower dorsolateral sulcus in which both lips are sharp and by the external genitalia. Females have the apical process and the posterior protuberance of the thelycum much narrower than in *P. a. aztecus* and *P. a. subtilis*, and in the males the ventral costa of the petasma is almost straight or only slightly curved rather than markedly convex distally; and also is armed close to the apex with a group of teeth of moderate size and irregularly set, instead of a compact, elongated patch of small teeth on the attached edge of the ventral costa as is typical of the two subspecies of *P. aztecus*. It also differs from *P. a. aztecus* by the shorter, shallower, and often interrupted median sulcus, and shorter third pereopod; and from *P. aztecus subtilis* by the broader adrostral sulci.

Burkenroad (1939) referred to this shrimp as *Penaeus aztecus* Ives "Form C," which he distinguished from the typical *P. aztecus* by characters other than the external genitalia; however, both the thelycum and particularly the petasma are characteristic. Consequently, I consider this southern *Penaeus* a distinct species. The female *P. aztecus* "Form C" recorded by Burkenroad from Pernambuco is most likely a specimen of *P. a. subtilis* in which the adrostral sulcus is narrow, the width at the lowest limit of its range of variation.

Penaeus aztecus subtilis new subspecies

(Fig. 2 a–b; Fig. 3 a–c)

Langostino amarillo, ("yellow shrimp"); camarón marrón ("brown shrimp"); short feelered prawn; sara-sara; camarão lixo, ("dark shrimp"); camarão branco ("white shrimp").

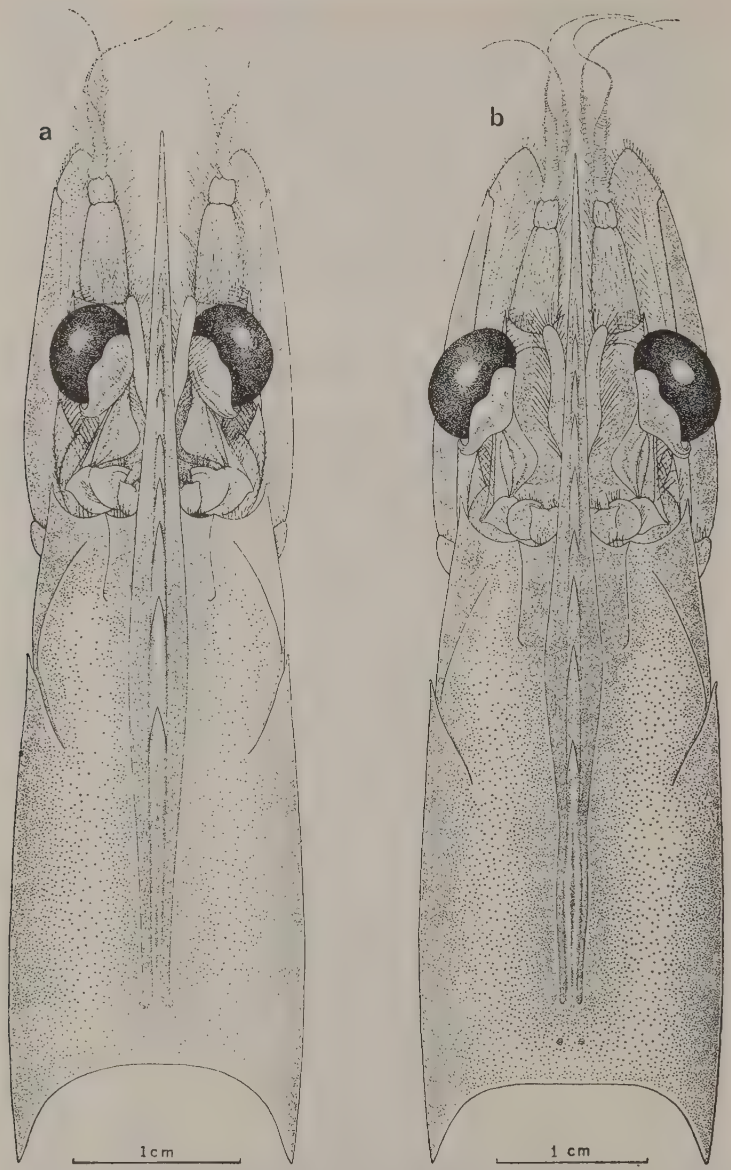
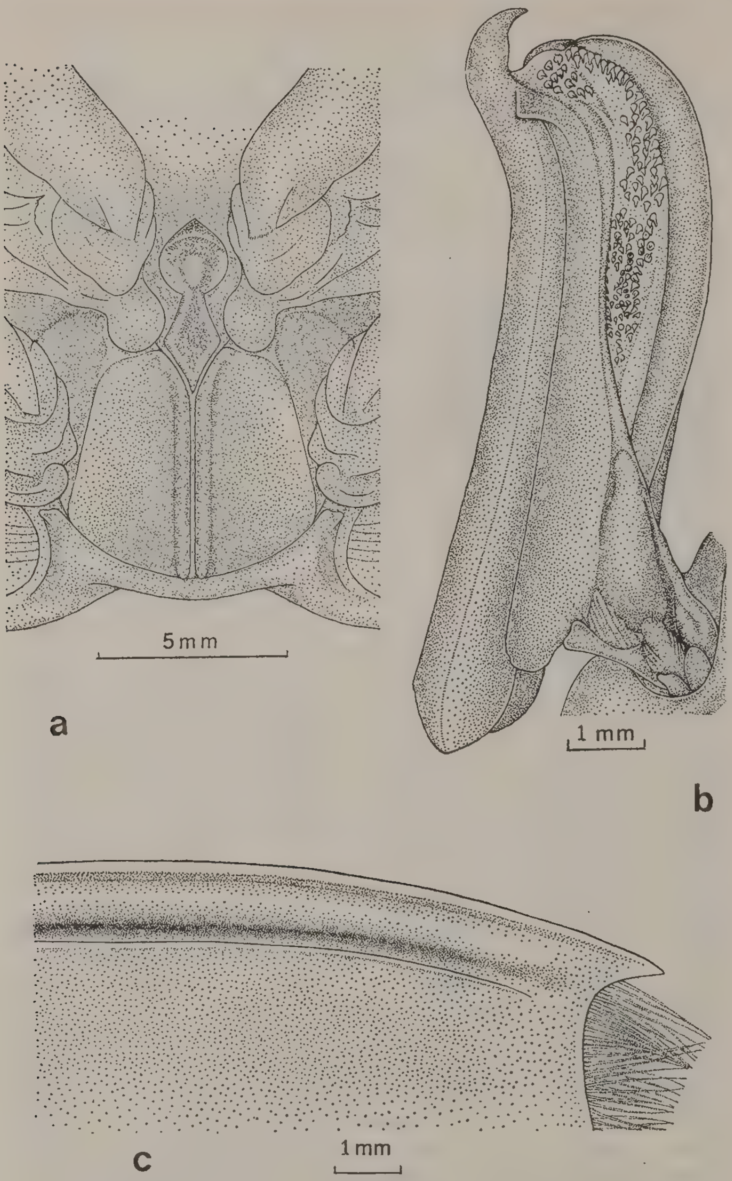


FIG. 2. *Penaeus aztecus subtilis* n. subsp. *a*, Carapace, ♀ 36 mm c.l., Gulf of Venezuela. *b*, Carapace, ♀ 35 mm c.l., off mouth Surinam River, Surinam.

Penaeus aztecus Ives, Burkenroad in part ("Form B"), 1939. Bull. Bingham Oceanogr. Coll. *6*: 34–52 Figs. 28, 29.

Holotype: ♂, USNM 119130, off Gallinas Point, Departamento de la Guajira, Colombia, 95 fms, 9 October 1965, *Oregon* Sta. 5685, 12°29′ NL, 71°54′WL.

Paratypes: CUBA: 1♀, USNM, Doctor Lagoon, Baracoa Beach, Havana, 1958, G. Mayor. 1♂, 2♀, USNM, Canímar River, Matanzas, 1954, C. Sánchez. 1♂, USNM, Key Francés, Caibarién, 300 fms [?], M. S. Roig. JAMAICA: 3♂, 1♀, YPM, western end Kingston Harbor, 4 feet, 1 February 1934. 5♂, 4♀, YPM, Kingston Market, 1 February 1934. 16 ♂, 11♀, USNM, 1–11 March 1884, *Albatross*. 1♂, 1♀, USNM, Montego River (1 mile from sea), 11 July 1916, C. B. Wilson. HAITI: 1♂, USNM, Port au Prince, 8 November 1965, A. Curtis. SANTO DOMINGO: 1♀, USNM, Puerto Plata, Ch. H. Fraser. PUERTO RICO: 3♂, 1♀, USNM, Mayagüez Harbor, 75–76 fms, 19–20 January 1899, *Fish Hawk*. 1♂, 4♀, USNM, Puerto Real, 26 January 1899, *Fish Hawk*. 1♂, 4♀, USNM, Hucares, 13–14 February 1899, *Fish Hawk*. VIRGIN ISLANDS: St. Croix: 12♂, 11♀, USNM, 27 January 1937, H. A. Beatty. 5♂, 3♀, USNM, Envy Bay, January 1938, H. A. Beatty. St. Johns: 5♂, 2♀, AMNH, *Antares* Expedition, W. Beebe. LESSER ANTILLES: Antigua: 1♂, USNM, English Harbor, 4–9 April 1956, Smithsonian Bredin Expedition, Sta. 83–56, F. A. Chace and D. V. Nicholson. 1♀, USNM, Tank Bay, English Harbor, 3 April 1956, Smithsonian Bredin Expedition, Schmitt, Chace, Nicholson and Jackson. St. Lucia: 3♂, 7♀, USNM, Port Castries, 2 December 1887. ARUBA–CURAÇAO: 1♂, USNM, off Aruba, 40 fms, 3 October 1965, *Oregon* Sta. 5656. Curaçao: 1♂, 2♀, USNM, 10–18 February 1884, *Albatross*. NICARAGUA: 1♂, USNM, Bluefields, 1965, A. Flores. PANAMA: 5♂, 6♀, USNM, Fox Bay, Colón, 3 January 1911, S. E. Meek and S. F. Hildebrand. COLOMBIA: Old Providence Island: 1♂, USNM, 4–9 April 1884, *Albatross* Sta. 2149–2150. 31♂, 23♀, YPM, Sabanilla, 16–22 March 1884, *Albatross*. 3♂, 7♀, USNM, off Puerto Colombia, 8–9 fms, 3 May 1964, *Oregon* Sta. 4867. 1♂, USNM, off Barranquilla, 75 fms, 17 May 1964, *Oregon* Sta. 4845. 2♂, 2♀, USNM, off Barrànquilla, 40 fms, 18 May 1964, *Oregon* Sta. 4851. 1♀, USNM, off Faro Point, 13–14 fms, 18 May 1964, *Oregon* Sta. 4849. 7♂, 3♀, USNM, off Faro Point, 60–65 fms, 18 May 1964, *Oregon* Sta. 4852. 1♂, 7♀, USNM, off Ciénaga, 50 fms, 17 May 1964, *Oregon* Sta. 4846. 1♀, USNM, off Cape la Vela, 100 fms, 1 June 1964, *Oregon* Sta. 4913. 2♂, 1♀, USNM, off Departamento de la Guajira, 105 fms, 8 October 1965, *Oregon* Sta. 5684. 1♂, 5♀, USNM, off Gallinas Point, Departamento de la Guajira, 95 fms, 9 October 1965, *Oregon* Sta. 5685. VENEZUELA: 27♂, 28♀, USNM, Barranquita, Lake of Maracaibo, 23 April 1964, J. J. Ewald. 8♀, USNM, Gulf of Venezuela, 12 June 1964, *Fioveca*, J. J. Ewald. 3♂, 6♀, USNM, off Las Piedras, Gulf of Venezuela, 26 fms, 5 October 1965,


5mm
a
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Oregon Sta. 5664. 1♀, USNM, off Mariusa Island, 13–15 fms, 26 August 1958, *Oregon* Sta. 2211. 5♀, USNM, off Boca Araguao, 9–10 fms, 27 August 1958, *Oregon* Sta. 2215. TRINIDAD: 1♀, USNM, off Casa Cruz, 20–22 fms, 26 August 1958, *Oregon* Sta. 2207. 1♂, 1♀, UMML, Icacos Point, March 1951, *Antilles*. 1♂, 1♀, UMML, Icacos Point, 19 January 1953, *Antilles*. 5♀, USNM, Gulf of Paria, February–October 1944, Anglo-American Caribbean Comm., R. T. Whiteleather and H. H. Brown. 2♀, USNM, Maturin Bar, off Point Barrial, Gulf of Paria, 26 April 1944, Anglo-American Caribbean Comm., R. T. Whiteleather and H. H. Brown. GUYANA: 1♂, USNM, off Marlborough, 20–25 fms, 30 August 1958, *Oregon* Sta. 2215. 3♂, 6♀, USNM, off Demerara Beacon, 11–22 July 1944, R. T. Whiteleather and H. H. Brown. SURINAM: 4♂, 7♀, USNM, off mouth Surinam River, 15 fms, 11 May 1957, *Coquette* Sta. 2. 1♂, 1♀, USNM, NE of mouth Surinam River, 30 fms, 30 May 1957, *Coquette* Sta. 36. 4♂, 1♀, USNM, NE of mouth Surinam River, 14 fms, 30 May 1957, *Coquette* Sta. 144. 1♂, USNM, between mouths of Coppename and Surinam Rivers, 15 fms, 6 June 1957, *Coquette* Sta. 172. 7♂, 13♀, USNM, off Surinam, 50 fms, 2 November 1957, *Oregon* Sta. 2016. FRENCH GUIANA: 2♂, 11♀, USNM, off Isère Point, 34 fms, 14 September 1958, *Oregon* Sta. 2322. BRAZIL: AMAPÁ: 4♀, USNM, Cape do Norte, 30 fms, J. F. Filho. PARÁ: 1♀, USNM, 100 miles off Cape Magari, 4 July 1965, J. F. Filho. 3♂, 25♀, USNM, off Salinopolis, 12 fms, 8 March 1963, *Oregon* Sta. 4215. PARÁ-MARANHÃO: 1♂, 1♀, USNM, June–July 1965, J. F. Filho. MARANHÃO: 2♂, 2♀, USNM, 27 June 1965, J. F. Filho. 1♀, USNM, off Paulino Neves, 20 fms, 11 March 1963, *Oregon* Sta. 4236. 12♂, 20♀, USNM, F. E. Sawyer. CEARÁ: 1♀, USNM, off Melancia, 20 fms, 16 March 1963, *Oregon* Sta. 4171. 1♂, 1♀, USNM, off Camocim, 15 fms, 12 March 1963, *Oregon* Sta. 4247. 1♂, USNM, off Camocim, 18 fms, 12 March 1963, *Oregon* Sta. 4250. 1♂, 1♀, USNM, Fortaleza, J. F. Filho. RIO GRANDE DO NORTE: 2♀, USNM, 1 February 1965, C. C. Neto. PERNAMBUCO: 10♂, 8♀, USNM, Public Market, San José, Recife, 10 August 1964, Ex. P. Alves Coêlho. ALAGOAS: 2♂, 2♀, MNHNP, Maceió, 2⅕–3¼ fms, 22 November 1961, *Calypso* Sta. 35. SERGIPE: 2♂, 6♀, MNHNP–USNM, off *Aracajú*, 26⅖–31⅓ fms, 23 November 1961, *Calypso* Sta. 42. 6♂, 14♀, USNM, mouth Agua Azeda River, Nossa Senhora do Socorro, 9 March 1966. BAHIA: 22♂, 18♀, USNM, Itaparica, 11 March 1966, A. Barreto. 6♂, MNHNP–

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FIG. 3. *Penaeus aztecus subtilis* n. subsp. *a*, Thelycum, ♀ 45.5 mm c.l., off Isère Point, French Guiana. *b*, Petasma, ♂ 34 mm c.l., off Gallinas Point, Departamento de la Guajira, Colombia. *c*, Sixth abdominal somite (posterodorsal portion), ♀ 36 mm c.l., Gulf of Venezuela.

USNM, off Bahia, 27–28 fms 24 November 1961, *Calypso* Sta. 35. Espirito Santo: 6♂, 10♀, MNHNP–USNM, Anchieta, 30 November 1961, *Calypso* Sta. 92. UNITED STATES: Florida: 1♂, YPM, Key Largo, 19 March 1934, M. B. Bishop, *Atlantis* [?].

Description: Rostrum long, reaching at least to distal end on antennular peduncle and at most to distal third of thickened portion of antennular flagellum, sinuous in shape, with apical portion markedly upturned. Adrostral sulcus (Figs. 2 a–b) narrow, width ⅕–¾ postrostral carina width, either tapering to a point posteriorly or turning laterally and broadening slightly at end, and usually short, ending ⅙–1/15 of carapace length from posterior margin of carapace. Median sulcus shallow, often interrupted, ending well anterior to posterior end of adrostral sulcus.

Dorsolateral sulcus (Fig. 3 c) variable in width, usually narrow; relation between keel height and sulcus width 2 to 8, modally 3.5.

Third pereopod relatively short, reaching only distal half of second antennular segment, at most exceeding peduncle by entire dactyl length.

Petasma (Fig. 3 b): Ventral costa curving proximally in gentle arc with distal portion unarmed along free border, two to three series of small teeth arranged in compact patch on attached border. Membranous portion of ventrolateral lobule extensively covered with spines. Distal fold of free margin of lateral lobe small, plain or armed with numerous spinules.

Thelycum (Fig. 3 a): Apical process projecting ventrally in sharp, broad, low-arched ridge which surrounds moderately concave surface with small knob usually present at center; posterior protuberance wide, with anteriorly bifurcate median carina, resulting ribs turning medially and converging at apical process, giving rise to diamondlike structure; surface enclosed by this structure plain or bearing median rib anteriorly, posteriorly or along entire length. Lateral plates with anteromedian angles divergent, leaving posterior protuberance exposed.

Color: *P. aztecus subtilis*, although of variable color, is most often brown, thus the name camarón marrón ("brown shrimp") in Venezuela, and camarão lixo ("dark shrimp") in Brazil. Yellowish specimens are rather common, and in some localities individuals are translucent pale yellow and are called camarão branco ("white shrimp") in Brazil.

Size: The largest female examined was 55 mm c.l., 205 mm t.l., and the largest male 36 mm c.l., 152 mm t.l. Holthius (1959) reported a larger male, 187 mm t.l.

Distribution: This subspecies ranges from Cuba along the arc of the Antilles, and from south of Cape Catoche throughout the Caribbean coast of Central and South America, and along the northern and eastern coast of South America, to at least Cape Frio, Brazil. Burkenroad (1939) identified and illustrated some specimens from "Rio de Janeiro."

Name: The name *subtilis* was suggested by the narrow and shallow adrostral sulci and the delicate, often indistinct and interrupted median sulcus.

Remarks: This subspecies differs rather strikingly from typical *P. aztecus*, the brown shrimp from the western Atlantic and the Gulf of Mexico. *P. a. subtilis* has a shallow, often interrupted and short median sulcus, instead of a deep, continuous, and long one as in *P. a. aztecus*; the adrostral sulci are very narrow and are either tapering or turned laterally posteriorly, rather than deep, long, broad, and of rather uniform width as they are on *P. a. aztecus.* The dorsolateral sulcus, although of variable width, is usually narrow, with a modal relation K/S of 3.5, whereas in *P. a. aztecus* it is wide, K/S modal 1.25. Finally, the third pereopod of *P. a. subtilis* is much shorter than that of *P. a. aztecus.*

P. a. subtilis may be separated from its close relative *P. paulensis* by the longer, sinuous rostrum and by the narrow adrostral sulcus. In males of *P. a. subtilis* the distal portion of the ventral costa of the petasma is strongly convex and armed with an elongated patch of closely set small teeth, very different from the almost straight costa provided with irregularly set, moderately strong apical teeth of *P. paulensis.* In females of *P. a. subtilis* the apical process and diamond-like structure on the posterior protuberance are much wider.

Burkenroad (1939) referred to this subspecies as *P. aztecus* "Form B." The study of extensive collections from throughout its range has indicated that it differs from *P. aztecus* from northern waters by constant characteristics; consequently I consider each population a geographical subspecies. Burkenroad, in the same publication, recorded one specimen of *P. aztecus* "Form B" from the Atlantic of "North America" and another (at Yale Peabody Museum of Natural History) from Key Largo, Florida. I have examined the latter, and it undoubtedly belongs to the southern subspecies; however, the accompanying label reads "*Atlantis,* March 19, 1934," and William C. Schroeder, from the Woods Hole Oceanographic Institute, has kindly informed me that the *Atlantis* was at Woods Hole on that date. It seems most unlikely that the error can ever be rectified. I strongly doubt that either of the North American specimens has been labeled correctly, because in the enormous collections from the northwestern Atlantic examined, I have not found the southern subspecies nor is there any reference in the literature other than Burkenroad's to its presence in northern waters.

The population of *P. a. subtilis* extending from the Gulf of Paria approximately to off Camocim, Brazil, shows some characteristics by which it can usually be distinguished from the population of this subspecies from the Caribbean region and that from northern South America and eastern Brazil. The former has the adrostral sulcus shorter (ending ⅙ to 1/11 of the carapace length from the posterior margin of the carapace), much shallower, and more tapering posteriorly; also the rostrum is longer and more distinctly sinuous. Many individuals, however, have a faint linear indication of the posterior portion of a longer adrostral sulcus. In addition, at both ends of the range of this population (in the Gulf of Paria and off Camocim), specimens showing the above characters are intermingled with specimens that have a longer and wider adrostral sulcus and a slightly shorter and less sinuous rostrum. Furthermore, in Colombia and Venezuela, the ranges of variation of the length and width of the adrostral sulcus and the length of the rostrum intergrade with those characters in specimens from the Gulf of Paria to northeastern Brazil. Too, the relation K/S ranges to a higher value in the latter population (2–8) than in the former (2–5); K/S modal value is almost the same, however, in both: 3 and 3.5, respectively. It thus seems that these are different populations of *P. a. subtilis* and that environmental conditions might be acting to produce the characters observed.

Penaeus duorarum notialis new subspecies

Fig. 4 a–d

> Camarón acaramelado ("candied shrimp"); langostino amarillo ("yellow shrimp"); camarón rosado sin mancha ("pink spotless shrimp") camarón cocinero ("cook shrimp"); camarón carbonero, ("coal carrying shrimp"); langostino or camarón rosado ("pink shrimp").

Penaeus brasiliensis: auct. in part; not *Penaeus brasiliensis* Latreille, 1817.

Penaeus duorarum Burkenroad in part ("Form B"), 1939. Bull. Bingham Oceanogr. Coll. 6, art. 6: 31–52, Figs. 18, 19, 26, 27.

Holotype: 1♂, USNM 119132, off Las Piedras, Gulf of Venezuela, 26 fms, 5 October 1965, *Oregon* Sta. 5664, 11°44′NL, 70°22′WL.

Paratypes: CUBA: 2♂, 3♀, CIP, Mariel, 17 November 1953, I. Pérez Farfante. 1♂, USNM, Cape San Antonio–Cape Cajón, 2–12 fms, 24 May 1914, *Thomas Barrera*. 3♂, 3♀, USNM, Doctor Lagoon, Baracoa Beach, 1952, J. Mayor. 1♂, YPM, Siguanea Bay, Island of Pines, 6 April 1925, *Pawnee*. 1♂, 1♀, USNM, Siguanea Bay, Island of Pines, 1954, G. Canet and I. Pérez Farfante. 23♂, 28♀, CIP, Gulf of Batabanó, 2–6 fms, December 1954, *Aida*, G. Canet and I. Pérez Farfante. 5♂, 7♀, CIP, Mouth Yumurí River, Matanzas Bay, 1954, C. Sánchez. 10♂,

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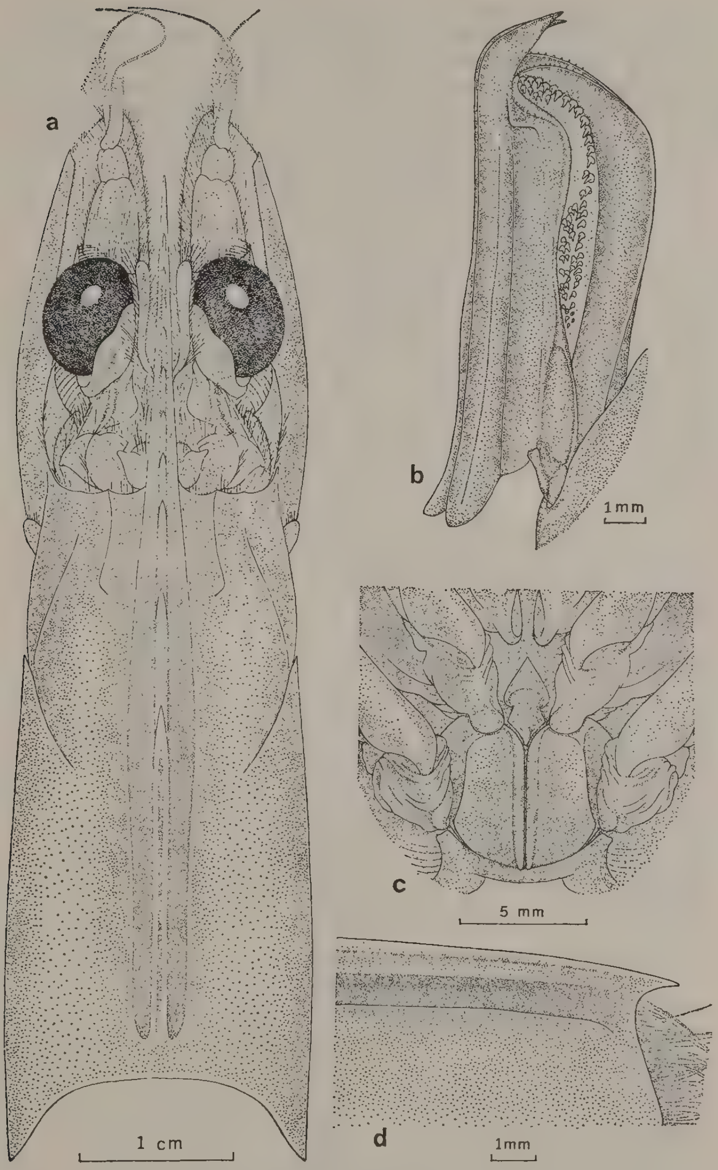
FIG. 4. *Penaeus duorarum notialis* n. subsp. *a*, Carapace, holotype ♂ 41.5 mm c.l., off Las Piedras, Gulf of Venezuela. *b*, Petasma, ♂ 34 mm c.l., off Las Piedras, Gulf of Venezuela. *c*, Thelycum, ♀ 38 mm c.l., off Las Piedras, Gulf of Venezuela. *d*, Sixth abdominal somite (posterodorsal portion), ♀ 42 mm c.l., off Great Pedro Bluff, Jamaica.


a
b
1mm
c
5 mm
d
1mm
1 cm

38♀, CIP, Tunas de Zaza, 17 June 1954, *Camarón* II, G. Canet and T. Sánchez. 3♂, 2♀, USNM, Cienfuegos Bay, 1954, G. Canet and I. Pérez Farfante. 1♂, 4♀, CIP, Nuevitas, 1954, J. Suárez Caabro. 6♂, 22♀, CIP, Sevilla Keys, August 1955, *Camarón* II, G. Canet and I. Pérez Farfante. 1♂, YPM, Guantánamo Bay, 22 April 1933, *Atlantis*. JAMAICA: 21♂, 31♀, USNM, 1–11 March 1884, *Albatross*. 1♂, YPM, 1–11 March 1884, *Albatross*. 1♂, 6♀, YPM, Kingston Market, 1 February 1934. 4♂, YPM, Kingston, 26 February 1937, I. H. Olsen. 9♂, 5♀, USNM, 22 fms, 15 May 1962, *Oregon* Sta. 3545. 8♂, 5♀, USNM, off Great Pedro Bluff, 11–12 fms, 18 May 1965, *Oregon* Sta. 5395. 141♂, 71♀, USNM, off Great Pedro Bluff, 12–13 fms, 18 May 1965, *Oregon* Sta. 5396. HAITI: 12♂, 6♀, AMNH, Bizeton, 1 March 1927, W. Beebe. 1♂, 1♀, AMNH, Port au Prince, 1927, W. Beebe. PUERTO RICO: 2♀, USNM, off San Juan, 40 fms, 29 September 1959, *Oregon* Sta. 2625. 1♀, USNM, Mayagüez Bay, winter 1965, *Carite*, P. W. Glynn. VIRGIN ISLANDS: TÓRTOLA: 1♂, 3♀, USNM, 27 fms, 27 September 1959, *Oregon* Sta. 2612. ST. CROIX: 2♂, 4♀, USNM, Kranse lagoon, H. A. Beatty. ST. JOHNS: 1♂, 1♀, AMNH, 1932, *Antares* Expedition, W. Beebe. ARUBA-CURAÇAO: 4♂, 2♀, USNM, 1937, P. W. Hummelinck. HONDURAS: 22♂, 20♀, USNM, off Ceiba, May 1966, R. Flores. 2♂, 1♀, YPM, Turneffe Cay, Gulf of Honduras, 21 April 1925, *Pawnee II*. 9♂, 12♀, USNM, Caratasca, May 1966, R. Flores. NICARAGUA: 2♀, USNM, Bluefields, 1965, A. Flores. PANAMA: 3♂, 3♀, USNM, Bocas del Toro, 15 fms, 28 April 1963, *Pelican* Sta. 800. 1♀, USNM, Fox Bay, Colón, 31 March 1911, S. E. Meek and S. F. Hildebrand. 3♂, 2♀, USNM, Fox Bay, Colón, 22 January 1912, S. E. Meek and S. F. Hildebrand. 6♂, 12♀, USNM, Fox Bay, Colón, 22 March 1912. 9♂, 1♀, YPM, Sweetwater River, Limón Bay, Canal Zone, 12 February 1934. COLOMBIA: 14♂, 23♀, USNM, Gulf of Urabá, 34 fms, 17 October 1965, *Oregon* Sta. 5728. 6♂, 6♀, USNM, off Cape Tiburón, Gulf of Darién, 43 fms, 18 October 1965, *Oregon* Sta. 5731. 6♂, 13♀, USNM, Gulf of Morrosquillo, 23 fms, 25 May 1964, *Oregon* Sta. 4886. 1♀, YPM, Sabanilla, 16–22 March 1884, *Albatross*. 10♂, 6♀, USNM, off Barranquilla, 40–50 fms, 19 May 1964, *Oregon* Sta. 4857. 1♂, 2♀, USNM, off Ciénaga, 50 fms, 17 May 1964, *Oregon* Sta. 4846. 1♀, USNM, off Departamento de la Guajira, 40 fms, 25 September 1963, *Oregon* Sta. 4395. VENEZUELA: 9♂, 10♀, USNM, off Las Piedras, Gulf of Venezuela, 26 fms, 5 October 1965, *Oregon* Sta. 5684. 10♂, 2♀, USNM, Gulf of Venezuela, 12 June 1964, *Fioveca*, J. J. Ewald. 1♀, UMML, off Boca Tuy, 1962, Tovar. 1♀, USNM, off Araguapiche Point, 2–22 fms, 26 August 1958, *Oregon* Sta. 2207. GUYANA: 1♀, USNM, off Demerara, 11–22 July 1944, Anglo-American Caribbean Comm., R. J. Whiteleather and H. H. Brown. SURINAM: 1♂, USNM, off westernmost end Surinam, 21 fms, 19 February 1963, *Oregon* Sta. 4169. 1♀, USNM, NE mouth Surinam River, 23 fms, 12 May 1957, *Coquette* Sta. 27. BRAZIL: MARANHÃO: 1♀, USNM, F. E. Sawyer.

Description: Rostrum relatively short, reaching at least distal third of second and at most distal end of third antennular segment, high and straight apically. Adrostral sulcus (Fig. 4 a) broad, ⅘ to 1½ postrostral carina width, wider at level of epigastric spine, width either uniform or slightly narrowing at posterior end, and long, ending 1⁄14 to 1⁄20 carapace length from posterior margin of carapace. Median sulcus deep along entire length, and long, ending immediately anterior to posterior end of adrostral sulcus.

Dorsolateral sulcus (Fig. 4 d) broad, relation between keel height and sulcus width ranging from 0.25 to 3, modally 1.75.

Third pereopod relatively long, exceeding antennular peduncle by half length of dactyl to ⅛ length of carpus.

Petasma (Fig. 4 b): Ventral costa broadening and turning proximally abruptly, distal portion armed with minute spines along free border and compact group of large teeth on attached border. Membranous portion of ventrolateral lobule with narrow band of spines, consisting of single series distally and three or four rows abreast proximally. Distal fold of free margin of lateral lobe small, either unarmed or with few marginal spinules.

Thelycum (Fig. 4 c): Apical process bordered by strongly convex, sharp ridge, surrounding rather strongly concave ventral surface. Posterior protuberance bearing single, prominent median carina, extending anteriorly toward apical process. Lateral plates with anteromedian corners slightly divergent, leaving median carina exposed.

Color: Although variable in color, *P. d. notialis* is most frequently light brown, thus the name langostino amarillo in Venezuela, and camarón acaramelado ("candied shrimp") in Cuba. In certain areas it is pink and is known as camarón rosado ("pink shrimp") and in others it is very dark brown and is called camarón carbonero ("coal carrying shrimp"), or camarón cocinero ("cook shrimp").

In the West Indies this subspecies, like the typical *P. duorarum* from northern waters, usually has a dark, reddish brown spot on each side at the juncture of the third and fourth abdominal somites. In northern South America, however, *P. d. notialis* consistently seems to lack these lateral spots.

Size: The largest female examined was 48 mm c.l., 192 mm t.l., and the largest male 41 mm c.l., 175 mm t.l.

Distribution: *P. d. notialis* ranges from Cuba throughout the Greater Antilles to the Virgin Islands, and from Belize, British Honduras, along the Caribbean coast of Central and South America, and the Atlantic coast of northern South America to São Luis, Brazil. It seems to be absent from northeastern Brazil, because it has not been reported nor have I found it in the series examined from Parnaiba to Bahia. *P. d. notialis* appears again in Ilheus and extends south to Cape Frio. There thus seem to be two discrete populations of "candied shrimp," one in the Caribbean Sea and Atlantic coast of northern South America, and another along the coast of eastern Brazil, from Ilheus to Cape Frio.

This subspecies is very abundant in some areas in the Caribbean region, apparently is extremely scarce along the Guianas and northern Brazil, but becomes abundant again in the southernmost portion of its range.

Name: The name is from the Latin *notialis*, meaning *southern*, and refers to its distribution in relation to typical *P. duorarum*.

Remarks: The dorsolateral sulcus of *P. d. notialis* is wider than that of *P. d. duorarum* from the northwestern Atlantic and the Gulf of Mexico. Burkenroad (1939) pointed out this difference between the two stocks and called the latter "Form A" and the former "Form B." The biometric studies I made have indicated a highly significant statistical difference in the relation between the height of the keel and the width of the adrostral sulcus: in *P. d. notialis* K/S ranges from 0.25 to 3, modally 1.75, in *P. d. duorarum* K/S ranges from 2.5 to 15, modally 4.5. In addition, overlapping is very limited; in only a few specimens of *P. d. notialis* from south Cuba does K/S reach 3, and in all the rest of the numerous specimens examined by me, including those from north Cuba, K/S is less than 2.5 *P. duorarum* from the Caribbean region and northern and middle portions of South America is distinct from *P. duorarum* from northern waters. It should be emphasized that the two stocks, each with a long pelagic larval phase, do not seem to mix across the Gulf Stream.

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Instantaneous Mortality and Maturation Schedules IBM 1620, Fortran II

This program computes instantaneous mortality and maturation rates from the general expression:

$$N_0 e^{-Mt_i} - \sum_{j=1}^{i-1} R_j e^{-M(t_i-t_j)} - R_i = 0$$

for $1 \leq i \leq 4$ and $j = 1, 2, \ldots, i{-}1$ where M = instantaneous mortality, N_0 = initial number of organisms in the population, R_j = number of organisms removed from or leaving the population at the end of the jth period, R_i = number of organisms remaining at the end of the final period, t_j = time in appropriate units to the end of the jth period, and t_i = time units to the end of the final period.

The derivation of this expression (in slightly different form) was presented by Parker (1962, p. 563) and Fredin (1964, pp. 554–555).

The program also yields: i) rate of survival, $(\sum_{j=1}^{i-1} R_j + R_i)/N_0$; ii) proportion of initial population that would have emigrated at the end of each period if no mortality had taken place, $R_j e^{Mt_j}/N_0$ and $R_i e^{Mt_i}/N_0$; iii) proportion of population remaining that emigrates at the end of each period, $R_j/(N_0 e^{-Mt_j} - \sum_{j=1}^{i-1} R_j e^{-M(t_j-t_{i-1})})$; iv) proportion of all surviving members that are removed or that emigrate at the end of each period. The output also includes a listing of input data.

An initial value for M is read in with input data, and a final solution is determined by an iterative process.

Execution time depends on the degree to which the initial value for M differs from the final value. Execution time on the IBM 1620 has averaged 10 seconds. The program required 20,292 storage locations.

Restrictions.—A maximum of four values may be used for R's (removals).

Availability.—A copy of the program listing with instruction sheet and sample output may be obtained free of charge from the Bureau of Commercial Fisheries, Biological Laboratory, Box 155, Auke Bay, Alaska, Attention Frances Pierce. A modified version written in FORTRAN IV for the IBM 7094 is also available.

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Returns of Hatchery-Reared Lake Trout in Southern Lake Superior, 1955–62[1]

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ABSTRACT

Experimental plantings of fin-clipped lake trout (*Salvelinus namaycush*) of various ages have been made in southern Lake Superior since 1952. The catch of planted lake trout by the commercial fishery was used to measure the success of stocking. Estimates of total returns were based on samples of 8.2 to 21.2% of the Wisconsin catches in 1955–62 and 36.4 to 46.8% of the Michigan catches in 1959–62. Marked lake trout were assigned to various plantings according to the fin mark, length of fish, readings of age from scales, and locations of capture.

Estimated returns from Wisconsin plantings of 9-month-old lake trout varied from 2.1 to 6.4%. Wisconsin releases of 16-month-old fish yielded returns of 5.7 to 37.3%. Returns from plantings in Michigan were 0.3% for 9-month-old fish and 1.5 to 3.8% for 16-month-old fish. The ratios of the returns from plantings of 16-month-old fish to those of 9-month-old fish were 3.9:1 for Wisconsin releases and 6.7:1 for Michigan releases. Lake trout planted in Wisconsin generally survived better than those released in Michigan. Returns from fish planted at ages of 17 to 40 months in Michigan in 1958–59 were far greater than those from 16-month-old fish released in Michigan, but were not as high as from the most successful plantings of 16-month-old fish in Wisconsin. Lake trout released in 1960 from shore and from boats survived equally well.

Average size of lake trout at release was more closely related to survival than any other factor. All except 1 of 10 highly successful releases were of fish larger than 22 per lb, and all 6 poor releases were of fish smaller than 34 per lb. Fish that ran 22 to 33 per lb survived only moderately well. A size of 17 to 20 fish per lb appears to be close to optimum.

Abundance of native lake trout, American smelt (*Osmerus mordax*), and sea lampreys (*Petromyzon marinus*) all appeared to be unrelated to stocking success. The only apparent method of rapidly improving the success of stocking is to rear all lake trout to an average size of 17 to 20 per lb.

INTRODUCTION

The sea lamprey (*Petromyzon marinus*) caused the near extinction of lake trout (*Salvelinus namaycush*) in Lakes Huron (Fry, 1953) and Michigan (Eschmeyer, 1957) and severely reduced the stocks in Lake Superior. Rehabilitation

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of lake trout stocks will depend on control of the sea lamprey, but rapid recovery also requires large-scale stocking. High survival of planted fish is needed because rearing facilities are limited in relation to anticipated requirements for hatchery-reared fish.

Before the 1930's, millions of lake trout fry, hatched from eggs taken from native fish, were planted annually in the upper Great Lakes. Fry stocking was gradually abandoned during the 1930's because the practice appeared to be ineffective (Dymond, 1957). In 1944–46 experimental plantings of 9-month-old fingerling lake trout were made in Lake Michigan, but returns ranged only from 0.06 to 0.67% (Cable, 1956). Sea lamprey depredations and collapse of the lake trout fishery contributed to an unknown degree to the low returns. In 1952–57 experimental releases of both fin-clipped and tagged hatchery-reared lake trout were made in Lake Superior to determine the best age for planting (Buettner, 1961). On the basis of these experiments, the age of 16 to 18 months appeared to be most economical.

The Michigan Department of Conservation undertook establishment of a lake trout brood stock in 1949. After successfully rearing the 1949 year-class for 4 years, the Department expanded the brood stocks to provide enough eggs by 1965 for annual plantings of 5.5 million yearling lake trout.

The Great Lakes Fishery Commission, through its contracting agents, the Fisheries Research Board of Canada and the U.S. Bureau of Commercial Fisheries, initiated control of the sea lamprey in Lake Superior in 1958 with a toxicant that selectively destroyed sea lamprey larvae in tributary streams. The Commission encouraged all governmental agencies to increase stocking of yearling lake trout and to mark all planted fish by clipping fins. By 1962 spawning runs of sea lampreys in streams tributary to Lake Superior had been reduced roughly 80 to 85% and plantings of yearling lake trout had been increased to nearly 2 million annually. To aid the rapid recovery of spawning stocks, the commercial lake trout fishery was closed in mid 1962 to all but the minimum amount of fishing necessary for biological sampling.

Although hatchery-reared fish have contributed substantially to the abundance of lake trout in Lake Superior in recent years (over 50% of all legal lake trout caught in U.S. waters in 1964 and many spawning fish in 1963–64 were fin-clipped), the only published data on the success of stocking were some incomplete estimates of the returns from various plantings given in a progress report on lake trout studies (Great Lakes Fishery Commission, 1961). The purposes of this report are to present estimates of returns from various plantings to the commercial fishery, to evaluate the relative success of certain experimental plantings, and to examine factors related to survival of hatchery-reared lake trout in Lake Superior.

The total returns of fin-clipped lake trout in the commercial fishery are the best available measure of the "success" of stocking. Because planted lake trout in Lake Superior were not fully vulnerable to commercial gear until 3 to 5 years after release, these data do not permit an actual assessment of survival even though rates of return are, obviously, related to survival. During the period covered by this study, sea lampreys competed with the commercial fishery for lake trout of vulnerable size and destroyed an unknown number. Fishing intensity was high enough, however, that large numbers of planted fish were taken in the fishery. Because rates of return are dependent on fishing effort, no estimates of total returns are given for the years since the season closure (1962). Data for 1962 are included because fishing effort increased that spring and raised the annual production to near the 1961 level in spite of the midyear closure.

MATERIALS AND METHODS

Field Procedures for Collection of Data

The Bureau of Commercial Fisheries and the Wisconsin Conservation Department took part in the intensive sampling of the commercial catches of lake trout in Lake Superior in 1959–62. The Bureau employed nine commercial fishermen in Michigan and one in Wisconsin to record data from their catches. Wisconsin Conservation Department employees accompanied most of the lake trout fishermen in Wisconsin, on a rotating schedule, to check their catches. All lake trout caught (except live undersized fish, which were released in conformity with usual fishing practices) were examined for clipped fins and sea lamprey wounds or scars. Data on total length (inches) and missing fins were recorded for all marked fish. Either entire catches or net-run samples of fish were measured and scale samples were taken periodically. Records were kept on location, depth of water, amount of gear lifted, and total number and weight of legal-sized[3] lake trout caught. Lake trout fishing was done mainly with large-mesh ($4\frac{1}{2}$–$4\frac{3}{4}$ inch, stretched measure) nylon gill nets, but a small part of the Wisconsin production came from pound nets from which all undersized fish were released. Samples were obtained from nearly all major fishing grounds in Michigan and Wisconsin (Fig. 1). In 1959–60 several additional commercial lake trout fishermen in Michigan voluntarily kept records from their catches. These data agreed closely with those collected in the same sampling areas by Bureau employees. The records obtained from all sampling areas of Fig. 1 were, therefore, considered representative of the production within the areas.

Complete records kept voluntarily by three commercial fishermen in Wisconsin in 1955–58 made possible an estimate of the total return of fin-clipped fish in Wisconsin for those years. A comparison of 1959–62 records of these fishermen with the entire Wisconsin samples indicated that their catches were representative of the entire Wisconsin production.

One Michigan fisherman at West Entry provided complete records of lake trout caught in small-mesh ($2\frac{1}{2}$–$2\frac{3}{4}$ inch gill nets fished for chubs (*Coregonus* [*Leucichthys*] spp.)), and Department personnel accompanied Wisconsin chub fishermen to obtain samples from small-mesh nets in 1959–60.

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[3] In Michigan the minimum size was $1\frac{1}{4}$ lb, dressed weight; in Wisconsin the minimum size was 17 inches total length. The two minimums were practically the same.

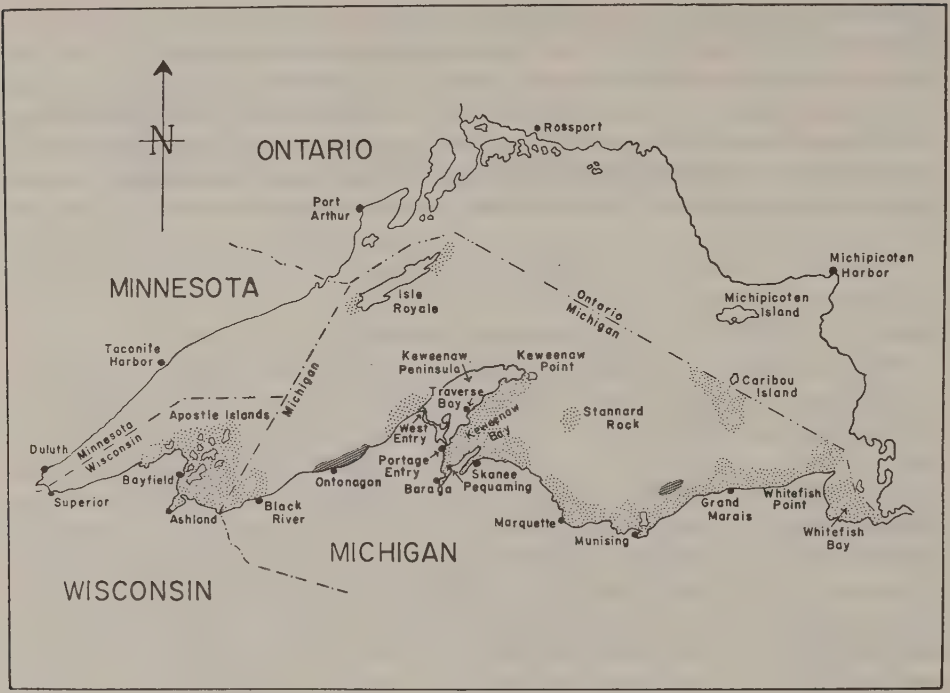
N
ONTARIO
Rossport
Port Arthur
MINNESOTA
Isle Royale
Ontario
Michigan
Michipicoten Harbor
Michipicoten Island
Taconite Harbor
Michigan
Keweenaw Peninsula
Keweenaw Point
Traverse Bay
Caribou Island
Stannard Rock
Apostle Islands
Minnesota
Wisconsin
Duluth
West Entry
Keweenaw Bay
Portage Entry
Bayfield
Ontonagon
Skanee
Pequaming
Baraga
Superior
Ashland
Black River
Marquette
Munising
Grand Marais
Whitefish Point
Whitefish Bay
MICHIGAN
WISCONSIN

FIG. 1. Major grounds fished for lake trout in Wisconsin and Michigan waters of Lake Superior, 1959–62. Samples were obtained from stippled areas in 2 or more years; no samples were obtained from crosshatched areas.

Wisconsin samples from large-mesh gear in 1955–58 amounted to 147,780 lb of legal-sized lake trout (Table I) and included 4077 fin-clipped fish. The 1959–62 samples totaled 86,543 lb and contained 11,775 fin-clipped fish. These samples constituted 8.2 to 11.2% (average, 9.4) of the annual Wisconsin production of lake trout in 1955–58 and 13.6 to 21.2% (average, 16.8) of the totals in 1959–62. Samples from large-mesh nets in Michigan waters in 1959–62 totaled 439,687 lb of legal-sized lake trout and 11,375 fin-clipped fish, and made up 36.4 to 46.8% (average, 39.1) of the production of lake trout in the areas for which estimates of returns were made. Offshore grounds near Isle Royale and Stannard Rock contributed only about 5% of the Michigan catches in 1959–62; samples from these areas contained so few fin-clipped fish that no estimates of returns were made.

The samples from small-mesh gear constituted 16.9% of all small-mesh nets fished in Wisconsin and at West Entry in 1959, and 8.0% of the total in 1960 (nearly all lake trout taken in small-mesh nets were undersized and were not reported in production statistics). Samples from small-mesh nets fished in other years and areas were inadequate for the estimation of returns of marked fish.

TABLE I. Production of lake trout (pounds, dressed weight), sample size, and percentage of production sampled in different areas, Lake Superior, 1955–62. (Areas listed are those for which estimates of returns were calculated.)

		Michigan							
Year and item	Wisconsin	Black River-Ontonagon	West Entry	Keweenaw Bay	Marquette	Munising-Grand Marais	Caribou Island	Whitefish Point and Bay	All Michigan areas
1955									
Production	552,690								
Sample	48,746								
Percentage	8.8								
1956									
Production	479,259								
Sample	53,582								
Percentage	11.2								
1957									
Production	286,765								
Sample	24,220								
Percentage	8.4								
1958									
Production	258,052								
Sample	21,232								
Percentage	8.2								
1959									
Production	181,966	14,951	8,311	225,553	61,359	227,385	52,429		589,988
Sample	24,694	7,292	8,311	67,035	24,095	55,602	52,429		214,764
Percentage	13.6	48.4	100.0	29.7	39.3	24.5	100.0		36.4

(Coutinued)

TABLE I. Production of lake trout (pounds, dressed weight), sample size, and percentage of production sampled in different areas, Lake Superior, 1955–62. (Areas listed are those for which estimates of returns were calculated.) — (*Concluded*)

Year and item	Wisconsin	Michigan							
		Black River-Ontonagon	West Entry	Keweenaw Bay	Marquette	Munising-Grand Marais	Caribou Island	Whitefish Point and Bay	All Michigan areas
1960									
Production	108,649	6,694	4,742	108,104	21,791	63,666	50,450		255,447
Sample	16,900	1,771	4,742	29,289	5,570	12,146	50,450		103,968
Percentage	15.6	26.5	100.0	27.1	25.6	19.1	100.0		40.7
1961									
Production	102,526	5,366	8,373	69,705	20,010	36,267		14,457	154,178
Sample	21,713	1,224	6,908	23,827	7,231	13,696		9,203	62,089
Percentage	21.2	22.8	82.5	29.3	27.7	37.8		63.7	40.3
1962									
Production	121,202	6,365	4,259	71,328	13,634	20,625		9,629	125,840
Sample	23,236	1,669	4,061	30,518	5,077	11,629		5,912	58,866
Percentage	19.2	26.2	95.4	42.8	37.2	56.4		61.4	46.8
Total 1955–58									
Production	1,576,766								
Sample	147,780								
Percentage	9.4								
Total 1959–62									
Production	514,343	33,376	24,685	474,690	116,794	347,943	102,879	24,086	1,125,453
Sample	86,543	11,956	24,022	150,669	41,973	93,073	102,879	15,115	439,687
Percentage	16.8	35.8	93.5	31.7	35.9	26.7	100.0	62.8	39.1

ESTIMATION OF RETURNS

Monthly production statistics from large-mesh gear by port were obtained from records of the Wisconsin Conservation Department and the Michigan Department of Conservation. Statistics on fishing effort for small-mesh gear were obtained from the Wisconsin Conservation Department. All production from large-mesh nets was assigned to the corresponding sampling areas (Fig. 1). Estimates of total catches of fin-clipped fish were made by 1-month periods for Wisconsin, but samples were not available for all months at all ports in Michigan. The percentage and size composition of the various groups of marked fish in the Michigan catches changed little within the periods of January–July, August–September, and November–December (the lake trout fishing season was closed during most of October). Estimates for Michigan waters were made for these sampling periods.

Returns were assigned to the various plantings on the basis of fin mark, length of fish, location of recapture, age of fish, or various combinations of these criteria. Ages of a total of 2192 fish were determined from plastic impressions of scales. Because fish from some of the early plantings could not be identified as to year of release, some groups planted in successive years at one location were combined and treated as single releases. A few groups were separated on the basis of location of capture in relation to the planting sites. These separations were based on known movements of planted lake trout (Pycha et al., 1965).

Estimates of total catches of fin-clipped lake trout (Table II) were made by simple proportion. The ratio of the pounds of legal fish in a sample from large-mesh nets to the total production of the sampling area was multiplied by the number of fin-clipped lake trout, both legal and undersized, from each planting in the sample to yield an estimate of the total catch from each release in that gear. No samples were taken at Ontonagon, but estimates of returns from that port were based on the assumption that the percentage of marked fish from each release in the catch was the mean of the percentages at Black River and West Entry (Fig. 1). Estimates of returns in small-mesh nets were made in a similar manner, but were based on the ratio of the amount of gear used to take the sampled catches to the total gear fished. The estimate of returns in 1958 from the 1955 Wisconsin spring release was based on the assumption that the ratio between returns per unit of gear in small- and large-mesh nets was the same for this group in 1958 as for the 1956 Wisconsin release in 1959.

SOURCES OF BIAS OR ERROR

No estimates of returns were made for lake trout planted in Wisconsin or Michigan that moved into Minnesota or Ontario waters. The amount of underestimation caused by this movement is unknown, but limited data suggest it should be small except for releases in Whitefish Bay (Pycha et al., 1965).

Regeneration of fins or failure to recognize clipped fins could cause underestimates of returns. Although considerable regeneration can occur (Shetter, 1951), about 97% of all the undersized lake trout caught in inshore waters of

TABLE II. Estimated numbers of lake trout recovered from various 1952–56 Wisconsin plantings by the commercial fisheries of Wisconsin in 1955–62, and Michigan in 1959–62.

Season and year of release	Age at release (*months*)	Number planted (*thousands*)	Gear[a]	1955	1956	1957	1958	1959	1960	1961	1962	Total returns all gears: Number	Total returns all gears: Percentage	Weighted average percentage
Fall 1952–53	9	278.0	L	254	310	1,273	938	2,003	673	130	110	5,782	2.1	3.5
			S					65	26					
Fall 1954	9	142.3	L	64	80	460	1,486	4,063	2,130	280	279	9,084	6.4	
			S					167	55					
Spring 1952–54	16	284.3	L	1,625	3,484	4,753	2,604	2,785	914	163	18	16,346	5.7	15.2
			S					0	0					
Spring 1955	16	102.8	L	197	791	3,880	7,431	18,030	4,943	670	356	38,311	37.3	
			S				1,538	390	85					
Spring 1956	16	200.7	L		0	682	879	3,871	10,837	9,854	7,003	34,989	17.4	
			S					1,203	660					

[a] L = large-mesh, 4½–4¾ inch mesh gill nets and pound nets; S = small-mesh, 2½–2¾ inch mesh gill nets.

Wisconsin and Michigan in 1963–64 and over 99% of the legal lake trout caught in Whitefish Bay in 1964 had clipped fins. Such high percentages indicate that probably neither fin regeneration nor careless observation was a serious source of bias.

Because data were lacking on returns from Michigan waters before 1959, estimates of total returns from Michigan plantings of 1952–55 were serious underestimates and cannot be compared directly with totals for Wisconsin plantings of the same years. The lack of sampling in Michigan before 1959 also caused underestimates of returns from Wisconsin releases made in 1952–56 because many Wisconsin fish moved gradually eastward into Michigan waters (Pycha et al., 1965). The error was greatest for the earliest releases, but was probably not large for the 1955–56 plantings. The 1956 group made little contribution to Michigan catches until 1960, and it seems probable that the 1955 group contributed little in Michigan before 1959.

Fish planted in Wisconsin and at Marquette in the fall of 1954 and spring of 1955 were assigned to their respective releases according to whether they were captured west or east of the Keweenaw Peninsula (Fig. 1). This separation gave a slight bias toward underestimation for the Wisconsin groups and overestimation for the Marquette groups.

Differences in amount of gear fished per unit area of "lake trout water" in Wisconsin and Michigan could affect total returns from plantings made in these states. Fishing intensity per unit area of water less than 40 fath (where most lake trout were caught) was, however, about equal in the two states in 1959–62 and was not greatly different in 1957–58. Differences in fishing intensity, therefore, should have had little effect on the apparent relative success of plantings in the two states.

RETURNS OF MARKED LAKE TROUT

Returns from Wisconsin Plantings of 1952–56

Fin-clipped lake trout were planted in Wisconsin in 1952–56 to compare the survival of 9-month-old fingerlings released in the fall and 16-month-old yearlings released in the spring. All fish were planted among the Apostle Islands from boats.

Lake trout planted in Wisconsin as yearlings survived better than fish of the same year-classes planted as fingerlings. Percentage returns of fingerlings varied from 2.1 for the combined 1952–53 releases to 6.4 for the 1954 group and averaged 3.5 (Table II). Returns from releases of yearlings ranged from 5.7% for the combined 1952–54 plants to 37.3% for the 1955 group and averaged 15.2% for all releases.

Although the 1955 and 1956 releases of yearlings yielded similar numbers of fish to the fishery (Table II), the percentage returns (1955, 37.3%; 1956, 17.4%) were very different and their histories in the fishery were dissimilar. The 1955 group came into the fishery strongly in the fall of 1958, contributed over 18,000 fish in 1959, and then declined to a return of about 5000 in 1960 and 670 in 1961. The 1956 group came into the fishery in the fall of 1959, contributed about 11,000 fish in 1960 and nearly 10,000 in 1961, and still yielded 7000 in 1962. Fishing effort declined about 23% from 1959 to 1960 and nearly 10% from 1960 to 1961. Also, abundance of sea lampreys fell drastically in mid 1961 and remained low thereafter. The decline in fishing intensity undoubtedly reduced fishing mortality of the 1956 group and the additional year of high sea lamprey predation experienced by the 1955 fish probably caused much higher natural mortality than for the 1956 fish. The incidence of lamprey wounds and scars from the fall of 1959 to the spring of 1961 was similar to that in South Bay, Lake Huron, during 1948–51 (Fry, 1953), when natural mortality of lake trout rose from 25 to about 70%. The effect of these factors of mortality should have resulted in a higher percentage return for the 1956 release, but the early returns suggest that the 1955 group survived better in the first year after release and established an advantage that held until the sixth year.

RETURNS FROM MICHIGAN PLANTINGS OF 1952–55

Fin-clipped lake trout were planted from boats off Marquette, Michigan, in 1952–55, but no data on returns were available until 1959. Comparisons of returns in 1959–62 from plantings made in 1952–55 show that releases made in Wisconsin yielded much higher returns that those made in Michigan (Table III). The 9-month-old fish planted among the Apostle Islands yielded nearly 8 times as high a return in 1959–62 as the 9-month-old fish planted at Marquette (2.3% compared with 0.3%). The 16-month-old fish released in 1953–54 at Marquette yielded a slightly higher return than the Apostle Islands releases of 1952–54, but these groups are not comparable because they covered different

TABLE III. Estimated returns of lake trout planted in Wisconsin and Michigan in 1952–56, taken in large-mesh gill nets in 1959–62.

Year and location of release	Age at planting (*months*)	Number planted 1952–56	Returns 1959–62	
			Number	Percentage
1952–54				
Apostle Islands	9	420,300	9,688	2.3
Marquette	9	325,700	949	0.3
Apostle Islands	16	284,300	3,880	1.4
1953–54				
Marquette	16	203,800	2,974	1.5
1955				
Apostle Islands	16	102,800	23,999	23.3
Marquette	16	60,700	2,312	3.8
1956				
Apostle Islands	16	200,700	31,565	15.7

periods. Of the two plantings of 16-month-old fish in 1955, the Apostle Islands release yielded slightly more than 6 times the percentage return of the Marquette release (23.3% compared with 3.8%), even though some of the returns assigned to Marquette were probably of Wisconsin origin.

Although the possibility exists that fish planted at Marquette grew faster than Wisconsin fish and came through the fishery before sampling was begun in Michigan, records kept by one fisherman at Marquette in 1958–59 confirmed that fewer marked fish were caught in 1958 than in 1959. The 1959–62 returns, therefore, appear to reflect lower survival of the groups planted in Michigan.

Comparison of Survival of Yearlings and Fingerlings

Previous comparisons of spring and fall plantings indicated that yearlings survived roughly 9 to 10 times as well as fingerlings (Buettner, 1961). The more extensive data of the present study show that the advantage for spring-planted yearlings was not as great as previously reported. The average returns from fish of the 1952–54 year-classes released in Wisconsin in 1952–55 (Table II) were 3.5% for fingerlings and 13.8% for yearlings[4] — a ratio of 3.9:1 in favor of the yearlings. The data from releases off Marquette in the same years (Table III) show a 6.7:1 ratio in favor of yearlings. Webster et al. (1959) reported similar results for yearling and fingerling lake trout released in Cayuga Lake, New York, where yearlings survived 3.94 times as well as fingerlings. They concluded that, on a cost basis, planting fingerlings was as efficient as planting yearlings. Their yearlings were, however, larger in comparison with their fingerlings than was true for the Lake Superior fish. The ratio of costs of planting yearlings and fingerlings would be lower for Lake Superior.

"Success" of Lake Trout Stocking

The 1955 release which had a total return of 37.3% (Table II) probably provided a measure of nearly the maximum return from lake trout stocking. Natural mortality certainly accounted for some loss during the 4 to 5 years before these fish reached full vulnerability to the fishery, but little is known about natural mortality of lake trout — especially at the ages below vulnerability to a fishery. Annual natural mortality rates (n) that have been reported ranged from 22 to 70% for lake trout from various lakes and nearly all values were below 50% (Webster et al., 1959; Ricker, 1958).

A series of simple models with various constant values of n applied to the 1955 Wisconsin release showed that the estimated return could not have been attained if n exceeded 20%. The apparent differences in total annual mortalities of the 1955 and 1956 releases under conditions of high and low sea lamprey predation indicate that natural mortality due to lamprey predation was very high on the 1955 release after the fish reached age V. If losses to lamprey predation equaled fishing mortality after age V (in 1959–61), n could not have exceeded 10% in the years before age V. The incidence of lamprey wounds on lake trout in Wisconsin (and presumably natural mortality) was somewhat lower in the spring of 1959 than in the remainder of the 1959–61 period, but even if losses to lampreys were only half as great as fishing mortality, n could not have exceeded 15%. Had there been any large mortality of these fish due to handling during release or to failure of the fish to adjust from hatchery to lake conditions, too few fish would have survived to age V to yield the return actually obtained unless n was practically nil prior to age V or fishing mortality was extremely high after age V. For example, if 25% of the fish that were planted died soon after release and n was only 10% after this initial mortality, the 1959 return would represent a fishing mortality rate (m) of nearly 48% that year. If, as seems probable, n rose much higher than 10% in 1959 because of high lamprey predation, the 1959 return would represent an improbably high value of m. The fact that fishing effort had declined to only about 60% of normal by 1959 makes such values of m appear nearly impossible. Both initial mortality after release and natural mortality in the early years of life must, therefore, have been very low.

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[4] The return from the 1956 release was not included in this average because no corresponding release of fingerlings was made in the fall of 1955.

Even if initial mortality was nil and n was only 10%, the 1959 return represents a value of m high enough (33%) to cast some doubt on the validity of the estimated return. More recent Wisconsin releases have, however, also produced surprisingly high returns despite an extreme reduction in fishing effort since mid 1962. During 1964, when fishing effort was only about one-tenth as high as in 1959, approximately 3% of the 1960 release was captured by the fishery and checked by Department or Bureau employees. Had the fishery been operating at the 1959 level of intensity in 1964, the percentage return from the 1960 release might have been as high as from the 1955 release and could possibly have been higher. The estimate of the 1959 return, therefore, appears to be reasonable.

The high return from the 1955 Wisconsin release appears to have resulted from low natural mortality at all ages below V and from a high rate of exploitation.

Returns from Plantings Made in 1958–60

All lake trout planted in Lake Superior since the spring of 1958 were fin-clipped yearlings or older (no fin-clipped fish were planted in 1957), and were partially vulnerable to the gear in 1959–62. Although total returns from the 1958–60 releases are not comparable to totals for the 1952–56 plantings, useful comparisons can be made for fish of comparable ages or years at large.

Marked lake trout were released at five locations in Wisconsin and Michigan in 1958: among the Apostle Islands; off Marquette, Munising, and Grand Marais; and in Whitefish Bay. Returns from fish planted at Munising and Grand Marais could not be separated and were, therefore, combined (Table IV). The fish planted in Whitefish Bay were 17 to 21 months old at release; all others were 16 months old.

TABLE IV. Estimated returns of lake trout planted in Wisconsin and Michigan in 1958–60, taken in large-mesh gill nets in 1959–62.

Year and location of release	Age at release (*months*)	Number planted	Number returned 1959	1960	1961	1962	Total	Percentage return 1959–62
1958								
Apostle Islands	16	184,000	436	553	2,696	4,022	7,707	4.2
Marquette	16	60,000	29	292	844	326	1,491	2.5
Munising and Grand Marais	16	200,000	125	171	889	850	2,035	1.0
Whitefish Bay	17–21	38,000			1,316	974	2,290	6.0
1959								
Apostle Islands	16	151,100	0	162	482	1,553	2,197	1.5
Baraga	26	27,100	22	237	774	1,424	2,457	9.1
Marquette	26	13,400	77	457	707	617	1,858	13.9
Marquette	40	2,900	10	406	224	96	736	25.4
1960								
Apostle Islands	16	161,400		14	819	1,165	1,998	1.2
Pequaming	16	131,700		0	88	489	577	0.4
Baraga	16	128,800		0	107	491	598	0.5
Munising	16	132,600		0	32	491	523	0.4

Returns in large-mesh nets from the 1958 plantings (Table IV) were greater for fish released in the Apostle Islands region (4.2%) than at Marquette (2.5%). The large planting at Munising and Grand Marais the same year yielded a return of only 1.0%. The Whitefish Bay releases yielded the highest return (6.0%) of any release in 1958, and this figure may be a serious underestimate because substantial numbers from this group, taken in large-mesh nets in Ontario waters of Whitefish Bay, were not included in the estimated return. Date were too limited to estimate the return in small-mesh nets, but the capture of 241 fish of this group in three lifts of chub nets in Whitefish Bay in 1961 suggests that the return was large.

The only yearling lake trout planted in 1959 were released in the Apostle Islands region; the three releases in Michigan were of 26- and 40-month-old fish (Table IV). The lower percentage return from the Wisconsin release (1.5) than returns at comparable ages from the 1955, 1956, and 1958 Wisconsin releases (11.9, 2.7, and 2.0%, respectively) suggests only moderate success. The three groups of older fish planted in Michigan, however, yielded the highest returns of any releases in that state (9.1 to 25.4%). Because the 40-month-old fish were vulnerable to large-mesh nets 1 to 2 years before the 26-month-old fish, the return from the older group was more nearly complete. The actual survival of fish of these three releases may have been similar.

The early returns from fish planted in 1960 (Table IV) were very incomplete, but are useful for evaluation of planting methods. All releases before

1960 were made from boats, in water 5–25 fath deep (the depths preferred by native yearling lake trout). In 1960, the plantings off Pequaming in Keweenaw Bay and off Munising were made from boats, but those at Baraga and the Apostle Islands were made directly from shore. This sites at Baraga and the Apostle Islands were within 1 or 2 miles of 15-fath depths offshore and were areas without large numbers of predacious fish. The releases at Baraga (from shore) and off Pequaming (from boats) were made as a controlled experiment — they were at locations about 6 miles apart, the fish were a single hatchery lot divided into groups of identical size and age, and poposite ventral fins were clipped for identification.

The return in the third year at large for the 1960 Wisconsin fish planted from shore (0.7%) was over twice the return at the same age from the 1958 (0.3%) or 1959 (0.3%) Wisconsin releases from boats, and was exceeded only by that of the 1955 Wisconsin plant (3.8%). The fish released at Baraga and off Pequaming yielded closely similar returns in the third year at large, and the group planted by boat near Munising also had a similar percentage return (in 1963–64, however, the Munising group yielded many more returns than the other 1960 Michigan plants and may have been nearly as successful as the Wisconsin fish). Of the 1960 plantings, the group released in Wisconsin again produced greater percentage returns than those released in Michigan (Table IV).

Data from the 1960 plantings indicate that planting from selected shore sites was as efficient as planting from boats. Shore planting is far more economical than boat planting and involves less handling of the fish. The fish released from shore disperse to preferred depths within a few hours (Pycha et al., 1965).

FACTORS AFFECTING SURVIVAL OF PLANTED LAKE TROUT

Although the plantings considered in this study were not strictly comparable (because of differences in locations, seasons, and years of release, sources of eggs, rearing stations, diets, and size and age of fish at release), the percentage returns from the releases were more closely related to size of the fish at release than to any other factor. Records of the plantings listed in Tables II–IV, and of five more recent releases, provided information on the relation of size at planting to subsequent "success". Because data collected after closure of the fishery in 1962 were not comparable to those obtained in earlier years, precise quantitative ratings of success could not be made. Comparisons of catches per unit of effort at various ages in both experimental and commercial gear, in addition to the information on total returns, formed the basis of ratings (partly subjective) of the success of various plantings made in 1952–62 (Table V).

Lake trout in all but 1 of 10 plantings that were rated "excellent" or "very good" averaged 21 per lb or larger at release. Fish of releases rated "poor" or "very poor" averaged 35 per lb or smaller. Those of "good" or "fair" releases were in the range of 22 to 33 per lb. The relation between size at release and success (Fig. 2) shows that sizes of 17 to 20 per lb are close to optimum for stocking lake trout.

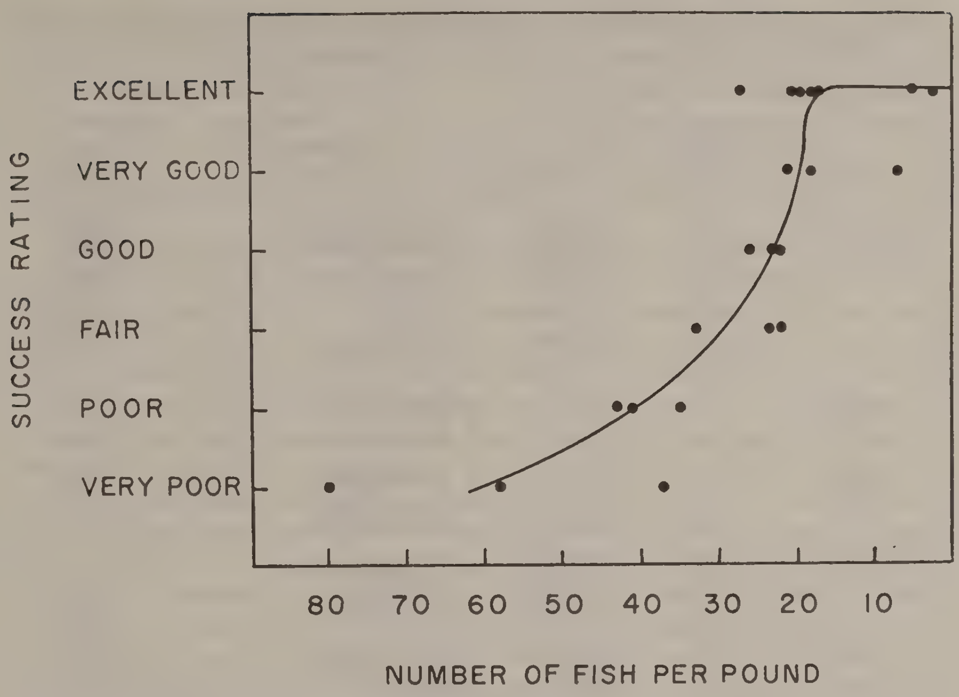

FIG. 2. The relation between size of lake trout at release and success of stocking. (Curve drawn by inspection.)

Although releases of yearlings in Wisconsin prior to 1960 were consistently more successful than those made in Michigan, the available evidence does not indicate that the cause was a more favorable environment in Wisconsin. In 1961, equal numbers of yearlings reared at the Salmo Hatchery in Wisconsin and the National Fish Hatchery in Michigan were released in Wisconsin (before 1961 all fish reared in Michigan were released in Michigan). About one-third of the Salmo Hatchery fish came from eggs taken from native Apostle Islands fish, but all other eggs came from brood stock held in Michigan. Fish from the two hatcheries were marked separately and were released in equal numbers at several shore sites (the National Hatchery fish were held 2 to 3 days in Wisconsin before release). The National Hatchery fish were larger (22 per lb) than the Salmo Hatchery fish (27 per lb) and the latter appeared to be in poor condition from disease the previous winter (about one-third of the fish had died in a 3-month period).

In 1964, commercial fishermen in Wisconsin and Michigan caught 1725 Salmo Hatchery fish and 593 National Hatchery fish — a ratio of 2.9:1 in favor of the fish reared in Wisconsin. The addition of partial returns from 1965, however, indicated the ratio will be about 2:1.

Planting National Hatchery fish in Wisconsin resulted in only usual returns for fish of the size released (Table V). Returns of the Salmo Hatchery

TABLE V. Qualitative rating of success, size of fish at release, and station of rearing for various plantings of lake trout in U.S. waters of Lake Superior. (Plantings arranged in rank order of success within rating categories.)

Rating	Number of fish per pound	Hatchery[a]	Location of release	Year released
Excellent	17	National	Whitefish Point	1961
"	20	Salmo	Apostle Islands	1960
"	18	Salmo	Apostle Islands	1955
"	2	National	Marquette	1959
"	5	National	Marquette	1959
"	20	National	Munising	1960
"	27	Salmo	Apostle Islands	1961
Very good	18	Salmo	Apostle Islands	1956
"	7	National	Keweenaw Bay	1959
"	21	National	Whitefish Bay	1958
Good	23	Salmo	Apostle Islands	1958
"	22	Salmo	Apostle Islands	1959
"	26	National	Keweenaw Bay	1961
Fair	23	National	Marquette	1955
"	33	National	Pequaming	1960
"	22	National	Apostle Islands	1961
Poor	35	National	Marquette	1958
"	41	Salmo	Apostle Islands	1952–53
"	43	National	Marquette	1953–54
Very poor	80	Salmo	Apostle Islands	1954
"	37	National	Munising, Grand Marais	1958
"	58	Harrietta	Whitefish Bay	1962

[a] National – National Fish Hatchery in Michigan; Salmo – Salmo Hatchery (state) in Wisconsin; Harrietta – Harrietta Hatchery (state) in Michigan.

fish were, however, exceptional and were higher than for two other groups of large Wisconsin fish. Heavy culling of the weaker fish by disease or possibly the all-meat diet fed during convalescence may have contributed to the high survival. Buettner (1961) reported that, of the two year-classes he studied, the 1954 year-class which suffered heavy mortality from "blue sac" and "white spot" diseases subsequently survived at least 1.5 times as well as the 1955 year-class which suffered only normal hatchery mortality.

Although the returns from the 1961 releases in Wisconsin suggested that fish reared at the Salmo Hatchery were hardier than those reared at the National Hatchery, the early results of the 1962 Wisconsin releases indicated only that size at release affects survival. Large (8.9 per lb) fish reared at the National Fish Hatchery and released in Wisconsin in early fall yielded percentage returns equal to those for large (18 per lb) fish reared at the Salmo Hatchery and released in late spring (partial 1965 returns totaled 0.22% for each group). Both groups of large fish showed a great advantage (4:1 ratio) over smaller (22.5 per lb) National Hatchery fish released in the same area in the spring.

Regular surveillance of several Wisconsin releases with both experimental and commercial gear has shown that success or failure of a planting is determined before early fall of the year of release (2 to 3 months after planting). The physiological "hardiness" of hatchery-reared fish at release could be an important factor in ability of the fish to adapt rapidly to lake conditions. Unfortunately, no measures of "hardiness" other than size at release have been determined.

No other factors were obviously related to success of stocking. Abundance of native lake trout, either large or juvenile, did not appear to be related to stocking success in 1952–61; highly successful releases were made in years of both high and low abundance of native fish. Data collected by experimental gear in Wisconsin since 1961, however, suggest that survival from plantings has declined as the number of fish released each year and abundance of both juvenile and legal-sized lake trout have increased (abundance of legal fish increased roughly threefold during 1961–65). Although American smelt (*Osmerus mordax*) eat the same food and are commonly at the same depths as juvenile lake trout, abundance of smelt appeared to be unrelated to returns from stocking. Sea lamprey predation undoubtedly reduced the total return from many releases, but changes in abundance of sea lampreys showed no relation to the success of various releases. Mortality during the first few months after release appeared to be far more important than sea lamprey predation in determination of the returns from a release. Lamprey predation appeared to be confined mainly to fish as large as or larger than the average size taken in commercial nets.

Although selective breeding of lake trout for rapid growth to increase the average size at release might appear to offer a possibility of improving success of stocking, the late maturity of lake trout (5 to 7 years in hatcheries) makes early results unlikely. The only method that clearly offers early improvement of stocking success is to rear lake trout to optimum size for release (17 to 20 fish per lb). Any alteration of rearing practices (including heavy culling of small, weak fish) that would advance attainment of this size should result in consistently higher success of planting lake trout.

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Format for Description of the Research Project in Biology

The project is a fundamental unit of administration in most research organizations, and its output forms a cluster of interrelated facts and ideas that is the unit of production of the organization. To meet the need of administrators, some form of description is normal for research projects. These descriptions range, with the organization and project, from occasional informal conversations to frequent formal written communication between scientists and their administrators.

The format described in this paper is a result, in part, of my interest in the possibilities for the formal programming of biological research projects by techniques such as the "Critical Path Method" and the "Program Evaluation and Review Technique" (Miller, 1963). A project described according to the format will display those elements common to most research projects in a standardized form. The standardized presentation will enable information on the project to be communicated to others and to be evaluated and programmed more efficiently than by *ad hoc* procedures. The areas of scientific procedure that are treated include literature review, alternative hypotheses, experimental design, and sampling methods. Needs of the project for time, personnel, space, and materiel are also described. An additional benefit of the format is that it serves as a proofing device against which the researcher can check the thoroughness of his planning.

The format is intended principally for field studies in ecology, growth, life history, and population characteristics of organisms and should be useful in a variety of other research, both applied and basic. Its use requires informative and succinct statements in response to its headings — sections that do not fit the research may be altered or deleted. The optimum time to prepare a written research design may vary with the project — sometimes detailed planning will be required before a project is started, but at other times such planning may not be needed until the results of a preliminary investigation are available.

Considerable effort will be required to describe the average project according to this scheme. A simple test demonstration of a small study under my supervision took more than a week to complete. But one may ask whether a considerable amount of time should not be spent in planning projects that possibly will involve thousands of dollars and the professional lives of many people. Also, the manner in which research is conducted could influence the attitude of other scientists and the general public for years to come.

The manuscript has received helpful comment from numerous scientists, and I have freely used their suggestions, so that in some respects the manuscript represents the work of a committee more than an individual. The paper will be justified if it stimulates further efforts on the subject.

Format and Explanations

Title Page

Give a descriptive title, the probable inclusive dates of the project, the author(s), and the date of submission of the plan.

I. Résumé

Briefly summarize the problem; state the facets of the problem that the project will illuminate or solve; and give the time schedule of the project.

II. General Description

A. Background

Give a general review of the scientific field involved, a brief history of its development, and its scientific or economic importance. Document with references to important works on the subject.

B. Research Methods and Objectives

Describe the research topic selected in more detail than is presented in the résumé and point out how the findings will apply to the problem described in the résumé. Clearly define the primary and ancillary research objectives.

III. Alternative Research Approaches

Give a brief objective analysis of practical alternative research pathways to solution of the problem. State why the alternatives were rejected in favor of the scheme selected.

IV. Structure of the Research

A. Institutional Involvement

How deeply will the research project involve the sponsoring institution? List the programs, projects, staff, and facilities that will be affected and the nature of the effects. Give the resources or facilities outside of the institution that will be used by the project.

B. Pertinent Scientific Fields

List the scientific fields and their subdivisions that are so pertinent that their literature should be consulted.

C. Extent of Coverage

Briefly state the limits of the project in terms of its geography and subject matter. For example, in a marine ecological study, what geographical area, depth range, and salinity range will be involved? Also, what biological communities will be investigated? What portions of the ranges and areas of subject matter will receive heavy, moderate, or light emphasis?

D. Steps to Objectives

Prepare a list or flow diagram of the questions to be answered or the hypotheses to be tested and the operational elements required to accomplish the desired goals. After each element elaborate briefly in terms of the item from the following list that most adequately characterizes the element and give the number of the item selected: The element has been demonstrated to be true or has been assigned reliable values in the literature (1), it is to be determined or verified during the project (2), it is assumed to be true and is indirectly supported in the literature (3a), and it is assumed to be true but is supported poorly or not at all in the literature (3b). Document the elements marked with (1), explain those marked with (2), and defend briefly those marked with (3a) or (3b) and explain why direct verification will not be attempted. Follow with a paragraph that highlights those parts of the project considered to be original.

E. Accuracy of Results

Give the degree of accuracy sought in the results, according to the following three-level scheme (Siegel, 1956). Briefly give the reasons for deciding on the particular level.

Level 1, Nominal. At this level, symbols, terms, or classifications are applied to objects or groups, but the information is so limited that the categories cannot be ranked and must be treated as equivalent.

Level 2, Ordinal or ranking. At this level, differences between objects or groups may be related by the symbols $<$ and $>$, but the information is not sufficient to satisfy the requirements of the interval scale (level 3, below).

Level 3, Interval. At this level, numerical distances between the values can be measured and a real number assigned to all objects in the ordered set. The data may be expressed in simple arithmetic form or as numerical transformations.

V. Methods

A. General Description

Briefly characterize the experimental and sampling methods.

B. Detailed Discussion

Give a full account of the experimental apparatus and the sampling devices, their methods of use, the sampling pattern in time and space, and the objects or materials to be sampled. If no experimental apparatus or sampling device is used, describe the methods of observation or survey. How will the accuracy and bias of the equipment or observers be established? Describe the experimental controls that may be practical. Give the criteria for adequate sampling for each type of datum to be gathered.

C. Processing and Storing Samples

Describe how the biological samples will be processed in the field and in the laboratory. Give the names of the people who will identify the specimens, the volumes of organisms to be handled, the places of analysis and storage, and the time schedule for analyzing the samples.

D. Analyzing the Data

Discuss the plans for analysis of the data. What types of numerical data will be involved (e.g., enumerative, ratios, continuous distributions)? Will the treatments be parametric or nonparametric? What interactions will be investigated? What statistical tests will be required? Is it likely that transformations of data will be required? What confidence levels will be employed? Give examples of similar analyses from the literature.

VI. Test of Expected Results

Valuable insight into the feasibility of a research project may be gained by a critical advance consideration of quantitative relationships that may be predicted for the data. For example, when an experiment is designed to measure the differences between samples, one should give considerable thought as to how significant the differences would be if they were found. How will degrees of difference be interpreted? Useful data can sometimes be obtained from the literature or from colleagues, and one can gain considerable insight concerning the practicality of his methods by inspecting these data as if they were his results. In other words, would the results expected actually give the answers sought? Be prepared to give examples and defend the logic.

VII. Schedule

A. Personnel

List the personnel and their minimum qualifications needed for each phase of the project. Give an estimate of the number of hours they will work per week and per month. Will work extend to nights or weekends?

B. Materiel

List all major apparatus and supplies that will be required. Give the required schedule for the supplies to be on hand and the apparatus to be functioning fully.

C. Research Timetable

Give a timetable for phases of the research. Include (1) completion of bibliography, (2) gathering of data, (3) analysis of data, and (4) completion of manuscript.

VIII. Costs

List all major costs and divide them into expenditures over the years the project is scheduled. Include cost of (1) permanent and temporary employees, (2) apparatus and supplies, and (3) miscellaneous.

IX. Tentative Titles of Publications

List titles, authors, and proposed outlets of publications that will result from the research. Give a brief description of what each publication will cover.

X. Safety

List the special hazards and hazardous situations that could develop. Follow each with a paragraph that describes the ways the hazard may be circumvented or neutralized and the safety procedure to be followed.

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Growth of Lake Trout in Lake Superior before the Maximum Abundance of Sea Lampreys

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Growth of Lake Trout in Lake Superior before the Maximum Abundance of Sea Lampreys

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ABSTRACT

The growth in length of lake trout (*Salvelinus namaycush*) from the inshore water of Lake Superior in 1953 increased with age from the 3rd to 9th year, and was nearly constant from the 9th to the 12th year. Growth was greatest in the 1st year (4.0 inches) and least in the 2nd and 3rd years (2.3 inches). Between the 4th and 9th years the increments increased from 2.6 to 3.5 inches. Growth was calculated from a curvilinear body-scale relation. Intraseasonal growth in length extended from late April until well after October; most growth was in late summer and fall. The younger fish started growth earlier, and some mature fish did not increase in length until after the October spawning. Lake trout reached the minimum legal weight (1.5 pounds) in the 7th year of life and the average size taken in the commercial fishery (about 3 pounds) in the 8th year. The annual increase in weight in the 8th year of life was over 64%. Fish used in this study grew more slowly than those from Lakes Michigan and Huron taken during the period when sea lamprey abundance was increasing, but at about the same rate as lake trout of Lake Michigan before the sea lamprey appeared.

INTRODUCTION

The lake trout (*Salvelinus namaycush*) was the most valuable species in the commercial fishery of Lake Superior before its drastic reduction by the sea lamprey (*Petromyzon marinus*), during the 1950's. In 1945–49 the average annual production of lake trout in the U. S. waters of Lake Superior was 3,139,400 pounds and although they contributed only 14 to 20% of the U. S. catch they made up 51 to 60% of the total value (Hile, Eschmeyer, and Lunger, 1951). Most of the U. S. production came from the inshore waters along the south shore.

At least three types of lake trout are found in Lake Superior. Lake trout that inhabit inshore areas are commonly called "lean" trout (*Salvelinus n. namaycush*), and deep water forms are known as siscowets or "fat" trout (*Salvelinus n. siscowet*). Lake trout from certain offshore shoal areas are known as "humpers." Some of the differences among the fish in these groups were given by Eschmeyer and Phillips (1965).

Although several publications have appeared on various life-history phases of lake trout in Lake Superior, growth studies have received little attention. Eschmeyer (1956) reported on growth during the first 3 years of life, Loftus (1958) gave average lengths of the age groups of river-spawning lake trout from certain Canadian waters, and Lawrie (1963) reported on intraseasonal growth of lake trout from Canadian waters. Rahrer (1965) described the growth of humper lake trout from the vicinity of Isle Royale. The present study deals with the growth of the lean lake trout from southeastern inshore waters of Lake Superior, before sea lampreys had become extremely abundant and lake trout stocks severely reduced.

MATERIALS AND METHODS

The study is based on 1,164 lake trout collected along the south shore of Lake Superior in Keweenaw Bay and in the vicinity of Marquette, Munising, and Grand Marais, Michigan, during February–October 1953 (Figure 1). Unless stated otherwise the samples from the various collection areas were combined because the data were similar or were insufficient to detect differences. Further justification for combining the areas appears from the data on hatchery-reared lake trout which showed considerable movement between adjacent areas where these collections were made (Pycha, Dryer, and King, 1965). Most of the fish were collected in experimental gill nets and trawls fished by the Bureau's R/V *Cisco*; others were taken from commercial gill nets and "float hooks." Collections from the various gears provided good representation of specimens over a wide range of length (Table 1).

Otter trawls fished by the R/V *Cisco* had

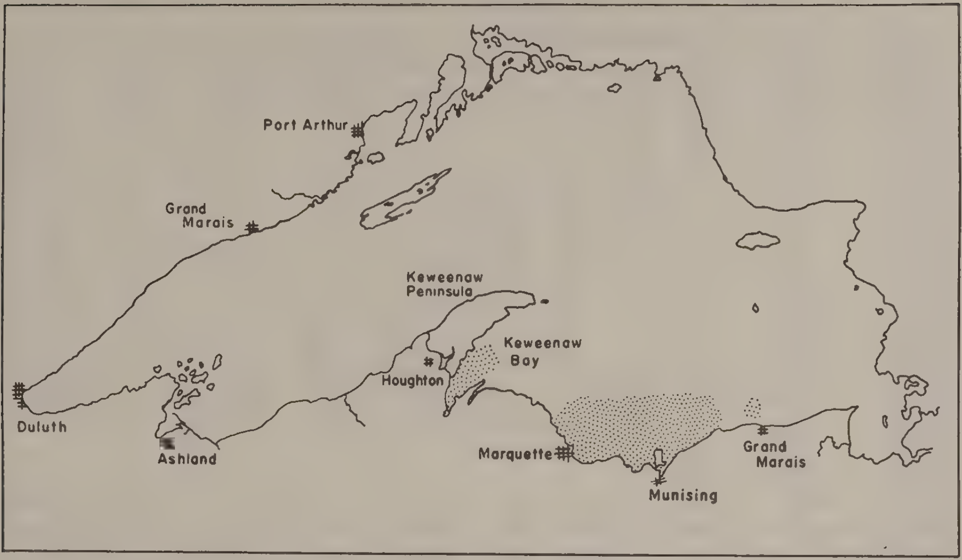

FIGURE 1.—Lake Superior. The stippled areas indicate the localities where samples were obtained.

a 35-foot headrope, were 36 feet long, with 1½- to 2½-inch mesh cotton body, and ½-inch mesh cod end. Mesh sizes of experimental nylon gill nets ranged from 1 to 6 inches and commercial gill nets were 4½- and 4¾-inch mesh. All mesh sizes are stretched measure. Float hooks were No. 6 hooks, usually baited with lake herring (*Coregonus artedi*), spaced 30 feet apart and suspended from a mainline floated about 12 feet below the surface.

The total length of each fish was measured to the nearest 0.1 inch. Scales taken from between the base of the dorsal fin and the lateral line were mounted and read as described by Rahrer (1965). Lengths at each annulus were determined from a nomograph constructed from the data on the body-scale relation.

Scales collected at or near the time of annulus formation were difficult to interpret. Some scales had partial circuli in the lateral fields before the year mark appeared anteriorly or posteriorly when the annulus was forming. I assumed that these circuli did not reflect growth in length because no increase in scale diameter could be measured along the anterior-posterior axis of the scale, which

TABLE 1.—*Length distribution of lake trout captured in experimental gear by the R/V* Cisco, *and by commercial fishermen*

Total length (inches)	Experimental gear		Commercial gear		Total
	Trawls	Gill nets	Float hooks	Gill nets	
3.0– 3.9	11	—	—	—	11
4.0– 4.9	59	—	—	—	59
5.0– 5.9	81	1	—	—	82
6.0– 6.9	39	35	—	—	74
7.0– 7.9	48	53	—	2	103
8.0– 8.9	29	42	—	1	72
9.0– 9.9	21	27	—	2	50
10.0–10.9	12	46	—	—	58
11.0–11.9	3	27	—	3	33
12.0–12.9	5	37	—	2	44
13.0–13.9	2	32	—	6	40
14.0–14.9	2	18	—	3	23
15.0–15.9	1	15	—	3	19
16.0–16.9	—	14	—	3	17
17.0–17.9	—	17	—	5	22
18.0–18.9	—	11	—	17	28
19.0–19.9	—	6	—	46	52
20.0–20.9	—	5	1	51	57
21.0–21.9	—	3	1	38	42
22.0–22.9	—	3	1	21	25
23.0–23.9	—	1	2	18	21
24.0–24.9	—	5	2	8	15
25.0–25.9	—	8	1	7	16
26.0–26.9	—	14	1	3	18
27.0–27.9	—	14	2	2	18
28.0–28.9	—	17	1	3	21
29.0–29.9	—	21	1	3	25
30.0–30.9	—	26	—	—	26
31.0–31.9	—	37	—	1	38
32.0–32.9	—	25	—	—	25
33.0–33.9	—	9	1	—	10
34.0–34.9	—	13	—	—	13
35.0–35.9	—	4	—	—	4
36.0–36.9	—	2	—	—	2
37.0–37.9	—	—	—	1	1
Total	313	588	14	249	1,164

TABLE 2.—*Length distribution of the age groups of lake trout*

Total length (inches)	Number of fish	Age group											
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
3.0– 3.9	11	11	—	—	—	—	—	—	—	—	—	—	—
4.0– 4.9	59	59	—	—	—	—	—	—	—	—	—	—	—
5.0– 5.9	82	78	4	—	—	—	—	—	—	—	—	—	—
6.0– 6.9	74	11	63	—	—	—	—	—	—	—	—	—	—
7.0– 7.9	103	—	82	21	—	—	—	—	—	—	—	—	—
8.0– 8.9	72	—	24	44	4	—	—	—	—	—	—	—	—
9.0– 9.9	50	—	3	36	11	—	—	—	—	—	—	—	—
10.0–10.9	58	—	—	42	16	—	—	—	—	—	—	—	—
11.0–11.9	33	—	—	12	19	2	—	—	—	—	—	—	—
12.0–12.9	44	—	—	3	34	7	—	—	—	—	—	—	—
13.0–13.9	40	—	—	—	21	17	2	—	—	—	—	—	—
14.0–14.9	23	—	—	—	6	15	2	—	—	—	—	—	—
15.0–15.9	19	—	—	—	3	12	4	—	—	—	—	—	—
16.0–16.9	17	—	—	—	—	9	8	—	—	—	—	—	—
17.0–17.9	22	—	—	—	—	3	15	4	—	—	—	—	—
18.0–18.9	28	—	—	—	—	4	19	5	—	—	—	—	—
19.0–19.9	52	—	—	—	—	—	16	32	4	—	—	—	—
20.0–20.9	57	—	—	—	—	—	11	33	11	1	1	—	—
21.0–21.9	42	—	—	—	—	—	9	22	11	—	—	—	—
22.0–22.9	25	—	—	—	—	—	—	8	15	2	—	—	—
23.0–23.9	21	—	—	—	—	—	—	2	16	3	—	—	—
24.0–24.9	15	—	—	—	—	—	—	—	11	4	—	—	—
25.0–25.9	16	—	—	—	—	—	—	—	10	6	—	—	—
26.0–26.9	18	—	—	—	—	—	—	—	2	12	4	—	—
27.0–27.9	18	—	—	—	—	—	—	—	—	13	5	—	—
28.0–28.9	21	—	—	—	—	—	—	1	—	10	6	4	—
29.0–29.9	25	—	—	—	—	—	—	—	—	11	12	2	—
30.0–30.9	26	—	—	—	—	—	—	—	—	1	23	1	1
31.0–31.9	38	—	—	—	—	—	—	—	—	2	24	12	—
32.0–32.9	25	—	—	—	—	—	—	—	—	—	12	13	—
33.0–33.9	10	—	—	—	—	—	—	—	—	—	2	6	2
34.0–34.9	13	—	—	—	—	—	—	—	—	—	—	10	3
35.0–35.9	4	—	—	—	—	—	—	—	—	—	—	3	1
36.0–36.9	2	—	—	—	—	—	—	—	—	—	—	—	2
37.0–37.9	1	—	—	—	—	—	—	—	—	—	—	—	1
Total	1,164	159	176	158	114	69	86	107	80	65	89	51	10
Average length		4.8	7.2	9.3	11.9	14.7	18.4	20.4	22.8	27.2	30.3	32.5	34.7

was used for calculations of growth in length. To distinguish new growth in length from that of the previous season, it was often necessary to compare the terminal growth increments during the growing season with completed growth increments determined by back calculations from older fish. All scales were read at least twice and the two ages usually agreed. Those which disagreed were reexamined and if a positive decision was not reached, the fish were excluded (only five fish).

LENGTH DISTRIBUTION OF THE AGE GROUPS

With few exceptions, the age of lake trout could be estimated to within one year if the length was known (Table 2). An average of 2.6 age groups were represented in each 1-inch interval. Only the two smallest and the two (poorly represented) largest 1-inch length intervals contained fish from one age group. A single age group, however, constituted at least 50% of the fish in each 1-inch interval with two exceptions (28.0–28.9 and 29.0–29.9). The length distribution of fish within age groups was broad. The average range between the longest and shortest fish of the various groups was 7.5 inches. Fish of age-groups I and II had ranges of only 4 and 5 inches, respectively, but all age groups older than II covered a span of at least 6 inches.

The length distribution of the age groups of spawning lake trout captured in the Marquette-Munising area provides a general description of the age composition of the spawning population, and the age and size at sexual maturity (Table 3). Age-groups VII through XII were represented in the spawning run; age-group X was most abundant (42% of the total). Age-groups IX, X, and XI made up 90% of all spawners, and 94% of all females. Males matured earlier and at a smaller length than females. The youngest mature male was age VII and the youngest female age IX; the smallest mature male was 22.2 inches and the smallest female 26.5 inches. The average lengths of the sexes within an age group did not differ greatly.

BODY-SCALE RELATION

The body-scale relation of lake trout was

TABLE 3.—*Length distribution of the age groups of spawning lake trout*

Total length (inches)	Number of fish	Age group and sex									
		VII	VIII	IX		X		XI		XII	
		♂	♂	♂	♀	♂	♀	♂	♀	♂	♀
22.0–22.9	2	1	1	–	–	–	–	–	–	–	–
23.0–23.9	1	–	1	–	–	–	–	–	–	–	–
24.0–24.9	4	–	3	1	–	–	–	–	–	–	–
25.0–25.9	4	–	2	2	–	–	–	–	–	–	–
26.0–26.9	14	–	1	8	3	2	–	–	–	–	–
27.0–27.9	13	–	–	11	1	1	–	–	–	–	–
28.0–28.9	15	1	–	7	–	6	1	–	–	–	–
29.0–29.9	21	–	–	10	1	8	2	–	–	–	–
30.0–30.9	26	–	–	1	–	15	8	–	1	1	–
31.0–31.9	37	–	–	1	1	17	7	6	5	–	–
32.0–32.9	25	–	–	–	–	10	2	6	7	–	–
33.0–33.9	9	–	–	–	–	1	–	5	2	1	–
34.0–34.9	13	–	–	–	–	–	–	8	2	2	1
35.0–35.9	4	–	–	–	–	–	–	–	2	1	1
36.0–36.9	2	–	–	–	–	–	–	–	–	1	1
Total	190	2	8	41	6	60	20	25	19	6	3
Average length		25.5	24.6	27.9	28.0	30.5	30.8	33.1	32.8	34.1	35.6
Average length, sexes combined		25.5	24.6	27.9		30.6		32.9		34.6	

determined from the average diameters of three scales from each of 1,157 fish (Table 4). To reduce error from small samples, seven fish of the three largest length intervals (35.0–37.9 inches) were excluded from the calculations. A graph of mean scale diameters and total lengths for each fish indicated a curvilinear relation (Figure 2). A logarithmic plot of the relation was not linear. Trial logarithmic plots of $L - a = c\ S^n$, for various values of a, indicated the relation was adequately described by the equation $L - 2.5 = 4.1019 \times 10^{-3}\ S^{1.54460}$. The equation was obtained by fitting a straight line by least squares to the logarithms of the average lengths minus 2.5 and the average scale diameters (×83) within each 1-inch length interval. Webster, Lund, Wahl, and Youngs (1960) reported a curvilinear body-scale relation for lake trout at Cayuga Lake.

TABLE 4.—*Relation between fish length and scale diameter of Lake Superior lake trout*

Total length[1] (inches)	Scale diameter (millimeters × 83)	Number of fish
3.6	39.9	11
4.4	51.6	59
5.5	72.5	82
6.4	83.4	74
7.5	99.1	103
8.3	110.7	72
9.5	126.2	50
10.4	137.3	58
11.5	143.9	33
12.4	158.7	44
13.5	166.4	40
14.4	173.7	23
15.4	182.8	19
16.4	200.6	17
17.4	207.8	22
18.5	217.2	28
19.5	223.0	52
20.4	230.0	57
21.4	234.3	42
22.3	244.4	25
23.4	247.9	21
24.5	260.3	15
25.6	264.8	16
26.4	278.0	18
27.5	282.4	18
28.5	289.1	21
29.5	289.6	25
30.4	302.9	26
31.4	305.1	38
32.5	319.1	25
33.4	306.5	10
34.3	325.3	13
35.6	316.0	4[2]
36.7	356.5	2[2]
37.7	314.0	1[2]

[1] Means for fish within 1-inch length intervals.

[2] These fish not included in body-scale regression calculations.

ANNULUS FORMATION AND SEASONAL GROWTH

Lake Superior lake trout show great individual variation in onset of the season's growth in length. The percentage of fish that showed new anterior-posterior scale growth tended to increase as the season progressed, but decreased with age at any given date (Table 5). The earliest collection that included fish with new growth was made on 28 April. The percentage of fish of all ages with new growth increased as the season progressed, from 2% in April to 93% in September, but declined to 45% in October. Some 60% of the October sample was composed of spawning-run fish (age-groups VII–XII) and fewer than 30% of these older fish had started growing. Among the spawning fish, evidence

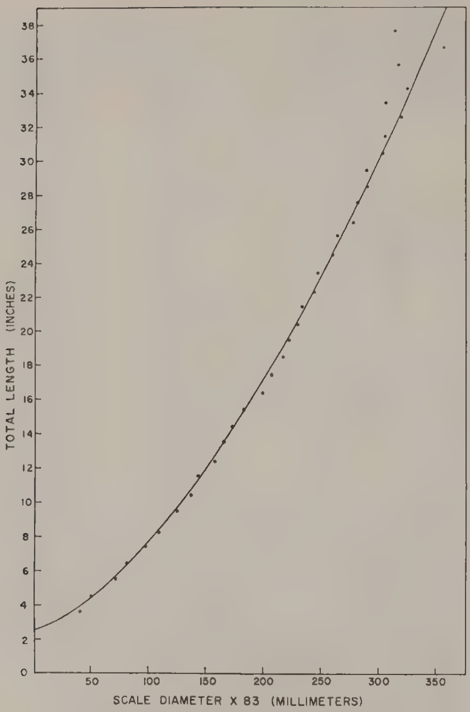

FIGURE 2.—Relation between total length and magnified scale diameter (×83) of lake trout. The curve represents the calculated scale diameters, and the dots the empirical average scale diameters.

TABLE 5.—*Percentage of lake trout with new anterior–posterior scale growth, by age group and date of collection. Number of fish in parentheses; none of the 145 fish captured in February and March had new growth*

Age group	Date of collection						
	Apr	May	Jun	Jul	Aug	Sep	Oct
I	—	50 (20)	100 (3)	100 (33)	100 (6)	100 (38)	100 (59)
II	—	50 (30)	52 (23)	100 (19)	100 (13)	100 (66)	100 (25)
III	—	54 (24)	18 (40)	100 (18)	100 (7)	81 (48)	94 (16)
IV	50 (2)	67 (27)	24 (46)	100 (4)	67 (6)	89 (16)	82 (11)
V	0 (2)	40 (5)	31 (13)	13 (16)	78 (9)	100 (7)	86 (7)
VI	0 (9)	7 (31)	9 (11)	0 (3)	—	75 (4)	0 (2)
VII	0 (15)	10 (21)	17 (6)	0 (2)	—	100 (1)	50 (2)
VIII	0 (20)	11 (9)	0 (3)	40 (5)	—	100 (1)	30 (10)
IX	0 (6)	0 (1)	—	0 (3)	—	—	18 (50)
X	0 (1)	0 (3)	—	0 (4)	—	—	11 (79)
XI	0 (1)	0 (1)	—	0 (1)	—	—	11 (45)
XII	—	0 (1)	—	—	—	—	22 (9)
All ages	1.8 (56)	36.4 (173)	26.9 (145)	72.2 (108)	90.2 (41)	93.4 (181)	45.1 (315)

of new growth in length consisted of the slight growth beyond the annulus or only one or two circuli. On some scales that did not show growth in length the annulus was forming on the lateral margins but was not visible in the anterior and posterior fields. The scales from spawning fish of known age (hatchery-reared fish that were fin clipped and released as yearlings) collected in October during recent years also showed little or no new growth. Thus, many older mature lake trout do not start their growth in length until late summer or fall and most may not grow in length until after spawning.

Cable (1956) reported that 93% of the known-age lake trout from Lake Michigan (ages II–VI) had started growing by the second half of July, and all of the fish had completed an annulus by the end of August. Only 72% of the fish from Lake Superior in age-groups II–VI had started growing in July and 89% had new annuli in August. It is not possible to state the date at which all Lake Superior fish had started growth. In the last collection that included fish in age-groups II–VI (October 15), 90% had started new growth.

The onset of growth of younger age groups may vary among areas. The percentages of fish in age-groups III and IV with new growth were 54 and 67%, respectively, in the May collections from Keweenaw Bay, but were only 18 and 24%, respectively, in the June collections near Munising. The data were inadequate for comparison of onset of growth at other localities.

Although the data on intraseasonal growth and length of the growing season were insufficient for detailed analysis, certain general trends were apparent. Of the fish which had resumed growing in any given month, the younger fish had completed a greater percentage of their growth than older fish (Table 5). For example, growing fish of age-groups I and II collected in October had completed an average of 63% of their average annual increments, but fish of age-groups IX–XII that had resumed growth in October had completed only 33% of their season's growth. The

Table 6.—*Calculated total length (inches) of 1,164 lake trout*

Age group	Number of fish	Length at end of year of life											
		1	2	3	4	5	6	7	8	9	10	11	12
I	159	4.1	—	—	—	—	—	—	—	—	—	—	—
II	176	3.9	6.3	—	—	—	—	—	—	—	—	—	—
III	158	3.9	6.4	8.7	—	—	—	—	—	—	—	—	—
IV	114	4.0	6.5	8.8	11.3	—	—	—	—	—	—	—	—
V	69	4.0	6.5	8.9	11.6	14.2	—	—	—	—	—	—	—
VI	86	4.1	6.5	9.1	12.0	15.0	18.3	—	—	—	—	—	—
VII	107	4.0	6.3	8.6	11.2	14.1	17.1	20.3	—	—	—	—	—
VIII	80	3.9	6.1	8.2	10.7	13.4	16.3	19.4	22.8	—	—	—	—
IX	65	3.9	6.0	8.2	10.7	13.6	16.7	20.1	23.4	27.0	—	—	—
X	89	3.9	5.9	8.1	10.5	13.2	16.3	19.7	23.1	26.5	30.1	—	—
XI	51	3.7	5.6	7.6	9.9	12.5	15.5	18.6	22.0	25.4	28.8	32.4	—
XII	10	3.6	5.4	7.2	9.3	11.8	14.5	17.4	20.6	24.4	28.0	31.1	34.5
Grand average calculated length		4.0	6.3	8.5	11.0	13.8	16.8	19.7	22.8	26.3	29.5	32.2	34.5
Increment of average		4.0	2.3	2.2	2.5	2.8	3.0	2.9	3.1	3.5	3.2	2.7	2.3
Grand average increment of length		4.0	2.3	2.3	2.6	2.8	3.1	3.2	3.4	3.5	3.5	3.5	3.4
Sum of average increment		4.0	6.3	8.6	11.2	14.0	17.1	20.3	23.7	27.2	30.7	34.2	37.6

growing season appears to extend from late April (earliest collection date for fish with new growth was 28 April) to well after 23 October (date of last collection). Fry (1953) reported that lake trout from South Bay, Lake Huron, had completed approximately one-half of their growth by mid-September and probably continued to grow until at least mid-October.

Evidence that the growing season extends into December, and that growth is substantial late in the year is shown by data in recent years on the returns of hatchery-reared lake trout. New year classes are recruited into the commercial catch slowly in August and September and rapidly in November and December. In some years, the mode of the length frequency of a single year class increases until at least mid-December.

The rate of intraseasonal growth and the length of the growing season may vary between localities. Although the fish of age-groups III and IV from Keweenaw Bay began growing earlier than those from Munising, a comparison of their growth from calculated lengths showed no differences. Since the calculated lengths of fish from the two areas were not different at various ages, it would appear that either the Keweenaw Bay fish complete their growth earlier or grow more slowly over a longer season. Extensive movements of fish between areas, as those described by Pycha, Dryer, and King (1965) for hatchery-reared lake trout in Lake Superior, however, could possibly conceal actual differences in growth for various areas.

Lawrie (1963) reported that the growing season of lake trout in some districts of Canadian waters of Lake Superior extended from March to late October or early November. He also noted differences in the intraseasonal growth of lake trout from the various districts along the Canadian shore. He suggested that these differences could be caused by variations in the onset, rate, and duration of growth in the groups of fish. His measurement of growth was based on the number of circuli formed outside the last annulus for fish of each age group, but the numbers of circuli were not related to growth in length of the fish, as in the present study.

CALCULATED GROWTH IN LENGTH

The calculated growth of Lake Superior lake trout showed some evidence of the effects of the commercial fishery on the growth history of fish of various age groups. Calculated lengths for each year of life decreased with increase in age for fish older than age VI (Table 6). This phenomenon has been attributed to various causes. If the population is exploited by a commercial fishery, the discrepancies may originate from gear selectivity which can cause progressive destruction of the faster growing fish of a year class as it enters and passes through the fishery. The onset of the progressive decrease in calculated lengths at age VII suggests that the intensive commercial fishery in Lake Superior may

Table 7.—*Calculated weights*[1] *and annual increments of weight of lake trout*

Year of life	Calculated weight (pounds)	Increment pounds	Percentage increase
1	0.02	0.02	—
2	0.06	0.04	200
3	0.16	0.10	167
4	0.38	0.22	138
5	0.78	0.40	105
6	1.45	0.67	86
7	2.55	1.10	76
8	4.19	1.64	64
9	6.50	2.31	55
10	9.56	3.06	47
11	13.49	3.93	41
12	18.26	4.77	35

[1] Calculated weights were computed by applying the general growth (sum of the average increments of Table 6) to the length-weight equation of lean lake trout of Eschmeyer and Phillips (1965). Their curve was based on fish collected in 1948–56 and included most of the fish of the present study; their data were in good agreement with the more limited data collected in 1953. Estimation of the weight of an age group based on the average length will usually result in a slight underestimate of the weight (Ricker, 1958).

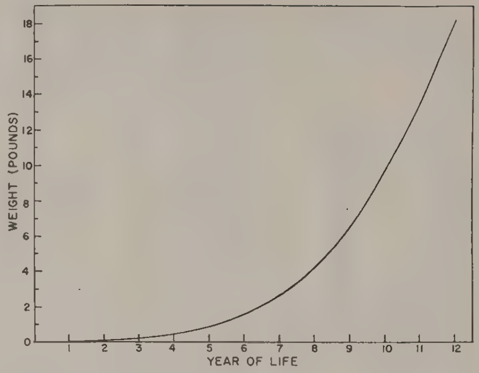

Figure 3.—Calculated growth in weight of lake trout.

have been the major factor there. Most fish younger than age VII were below legal size (1.5 pounds or about 17 inches), and were not fully vulnerable to the gears used in the fishery (Table 1). This apparent decrease of growth may also have been furthered by the selective predation of the sea lamprey on larger lake trout. Although sea lampreys had not become abundant in Lake Superior in 1953, a sharp decline in the commercial catch after 1952 indicated that the sea lamprey may already have been making inroads on the lake trout population.

Estimates of general growth in length (bottom of Table 6) were based on both grand average calculated lengths and the successive summation of grand average increments of length. Lengths computed from the sums of the increments were consistently larger than the averages of calculated lengths. The differences were 0.0–0.3 inches through the first 6 years, between 0.6 and 0.9 inches in the 7th, 8th, and 9th years, and from 1.2 to 3.1 inches in the 10th through 12th year. The sums of the grand average increments were considered the soundest estimate of growth because they avoid the irregularities caused by successive dropping of age groups and thus give a more realistic estimate of growth in the later years of life. Use of the increments also may lessen the effects of the selective destruction of fish with the more rapid growth. The sum of the increments might exaggerate the lengths at older ages, however, if the period preceding the year of collection were a series of years of increasing growth, which it could have been if the sea lampreys and the commercial fishery were reducing the lake trout stocks and the remaining fish grew faster each year.

Growth was greatest in the 1st year of life (4.0 inches) and least in the 2nd and 3rd years (2.3 inches). The grand average annual increments of length became progressively larger with increased age between the 3rd and 9th years (2.3 to 3.5 inches, respectively). Increments were 3.5 inches in the 9th–11th years and 3.4 inches in the 12th year. Lake trout reached 12 inches in the 5th year of life, 24 inches in the 9th, and 36 inches in the 12th year. They reached the minimum legal size near the end of the 6th year and became fully vulnerable to the commercial gill nets of 4½-inch mesh (at approximately 20 inches) near the end of the 7th year.

CALCULATED GROWTH IN WEIGHT

Annual increments of calculated weights of lake trout (Table 7) increased in every year of life and ranged from 0.02 pound in the 1st year to 4.77 pounds in the 12th (Table 7). Growth in weight (Figure 3) was relatively slow during the first 6 years but increased rapidly in the later years of life. Lake trout did not weigh one pound until the 6th year of life. They attained the legal weight of 1.5 pounds near the start of the 7th year of life

TABLE 8.—*Grand average annual increments of length (inches) of lake trout from Lakes Superior and Michigan calculated from curvilinear and assumed direct-proportion body-scale relations. Number of fish is in parentheses*

Year of life	Method of calculation, and lake			
	Curvilinear	Direct proportion		
	Superior 1953[1]	Superior 1953[1]	Michigan 1930–32[2]	Michigan 1947–52[3]
1	4.0 (1,164)	3.9 (1,164)	3.4 (811)	5.9 (1,319)
2	2.3 (1,005)	3.1 (1,005)	3.6 (811)	2.8 (1,319)
3	2.3 (829)	2.7 (829)	3.1 (804)	2.5 (1,280)
4	2.6 (671)	2.6 (671)	2.5 (495)	2.5 (1,025)
5	2.8 (557)	2.6 (557)	2.1 (155)	2.5 (293)
6	3.1 (488)	2.9 (488)	2.4 (40)	2.4 (13)
7	3.2 (402)	2.4 (402)	2.3 (12)	—
8	3.4 (295)	2.6 (295)	1.7 (3)	—
9	3.5 (215)	2.7 (215)	2.0 (1)	—
10	3.5 (150)	2.6 (150)	2.0 (1)	—
11	3.5 (61)	2.6 (61)	—	—
12	3.4 (10)	2.3 (10)	—	—

[1] Present study.

[2] Van Oosten and Eschmeyer (1956) grand average increments calculated from Table 20, page 41—fish collected in 1930–32.

[3] Cable (1956) grand average increments calculated from Table 20, page 40—fish collected in 1947–52.

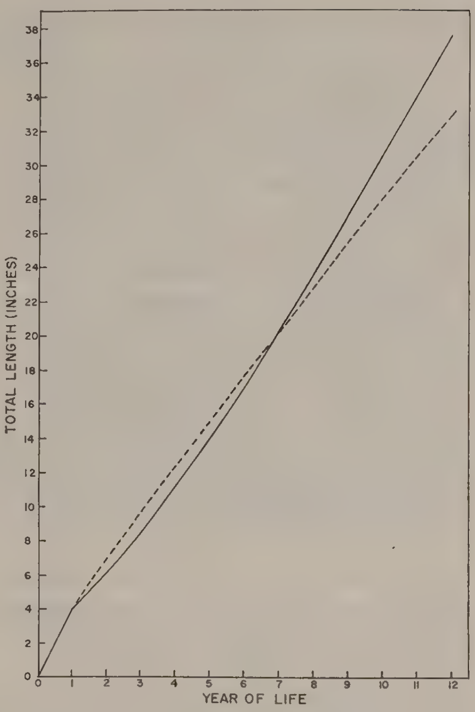

FIGURE 4.—Calculated growth in length of lake trout from the known curvilinear body-scale relation (solid line), and as computed by assumed direct proportion (broken line).

and more than doubled and redoubled the legal weight by the end of the 8th and 9th years, respectively. Their weight was over 18 pounds by the end of the 12th year—12 times the minimum legal weight.

Commercial fishermen along the south shore of Lake Superior report that the average weight of lake trout in the catch has been about 3 pounds for the past 20 or more years. Lake trout caught at 3 pounds in 1953 were at an age (8th year of life) where their annual increase in weight was over 64%. Although the natural mortality of lake trout from Lake Superior is unknown, loss of weight from natural death must have been less than gain through growth. A population that was exploited intensively could not have had high natural mortality and still have produced many fish that weighed in excess of 20 pounds. Capture of lake trout at a larger size almost surely would have increased the total production from Lake Superior. Smith and Van Oosten (1940) reached the same conclusion about lake trout of Lake Michigan, on the basis of their experiments with tagged fish.

INFLUENCE OF METHODS OF CALCULATION ON THE GROWTH CURVE

The growth of lake trout in this study was calculated by both direct proportion and from the actual curvilinear body-scale relation to permit comparison with other studies. The method of calculation clearly affects the estimates of growth (Table 8). Calculation of the lengths of Lake Superior fish by direct proportion lessened the differences among average increments and reversed the trend for fish to grow faster during the older ages (Figure 4). Two previous studies that reported calculated lengths of lean lake trout from the Great Lakes (Van Oosten and Eschmeyer, 1956; Cable, 1956), were based on direct-proportion calculations. In both studies the grand-average increments of length

TABLE 9.—*Growth in length (inches) of lake trout in various areas of the Great Lakes*[1]

Method of calculation and author	Area	Total length (inches) at year of life										
		1	2	3	4	5	6	7	8	9	10	11
Sum of grand average increments—based on known body-scale relation												
Rahrer (present study)	Lake Superior—southeast	4.0	6.3	8.6	11.2	14.0	17.1	20.3	23.7	27.2	30.7	34.2
Rahrer (1965) "Humpers"	Lake Superior—Isle Royale	3.5	5.1	6.9	8.5	10.4	13.0	15.4	17.6	19.8	22.1	24.3
Sum of grand average increments—based on assumed linear body-scale relation												
Rahrer (present study)	Lake Superior—southeast	3.9	7.0	9.7	12.3	14.9	17.8	20.2	22.8	25.5	28.1	30.7
Cable (1956)	Lake Michigan	5.9	8.7	11.2	13.7	16.2	18.6	—	—	—	—	—
Van Oosten and Eschmeyer (1956)	Lake Michigan	3.4	7.0	10.1	12.6	14.7	17.1	19.4	21.1	23.1	25.1	—
Average length at capture												
Rahrer (present study)	Lake Superior—southeast	4.8	7.2	9.3	11.9	14.7	18.4	20.4	22.8	27.2	30.3	32.5
Fry (1953)	Lake Huron—South Bay	—	10.9	13.8	17.9	20.4	22.9	24.6	—	—	—	—
Length at capture of spawning run fish												
Rahrer (present study)	Lake Superior—southeast	—	—	—	—	—	—	28.7	25.7	28.0	30.6	32.9
Loftus (1958)	Lake Superior—Montreal R.	—	—	—	—	—	24.9	28.0	31.0	32.3	33.0	33.4
Loftus (1958)	Lake Superior—Dog R.	—	—	—	—	—	20.0	25.2	26.0	26.6	28.4	29.3

[1] Data from Loftus based on lengths at capture read from Figure 4, page 266, of his paper; Cable's data are the sum of grand average increments calculated from Table 20, page 40, of her paper for fish collected in 1947–52; data of Van Oosten and Eschmeyer are sums of grand average increments calculated from Table 20, page 41, of their paper for fish collected in 1930–32. Fork lengths given by Loftus and Fry converted to total lengths by the formula: total length = 1.082 fork length + 0.045 inch.

changed little or decreased slightly with increasing age (Table 8). The grand-average increments of length derived from the curvilinear body-scale relation in the present study increased progressively in the early years of life and held steady in later years. The growth data derived from the direct-proportion method more closely approximate the growth reported from Lake Michigan.

GROWTH OF LAKE TROUT IN VARIOUS AREAS

Growth data for lake trout collected in Lake Superior in 1953 were calculated in different ways for comparison with growth of lake trout reported for other stocks in the Great Lakes (Table 9). Lake trout of the present study were longer at all ages than the "humper" lake trout from Isle Royale (Rahrer, 1965), both calculations based on body-scale relations. The lean lake trout ranged from 0.5 inch longer at the first annulus to nearly 10 inches longer at the 11th. The sums of the grand-average increments in length of Lake Superior lean trout calculated by direct proportion were all smaller than those from Lake Michigan reported by Cable (1956). Lengths reported by Van Oosten and Eschmeyer (1956) from Lake Michigan, however, were nearly the same through the first 7 years (less than 1 inch difference) but were smaller at 8, 9, and 10 years. The average lengths at capture of Lake Huron lake trout (Fry, 1953) were all larger than the length at capture for fish of the present study at the same ages. The largest difference was 6 inches at the end of the 4th year.

Lake trout from Lake Michigan (Cable, 1956) and Lake Huron (Fry, 1953) were taken in the late 1940's and early 1950's when the populations in these lakes had been reduced drastically by sea lamprey predation; the sparse populations may have contributed to faster growth than in Lake Superior. The data of Van Oosten and Eschmeyer for 1930–32, before the sea lamprey invaded Lake Michigan, suggest that normal growth in Lake Michigan may have been similar to that in Lake Superior.

River-run lake trout of Lake Superior from the Montreal River, measured at spawning time (Loftus, 1958), were larger in the 8th through 11th years than the spawning-run fish in this study, but those from the Dog River were all smaller than fish at the Montreal River and were mostly smaller than fish in my 1953 collections. These fish were taken in 1951–55 when numbers of lampreys were similar to those at the time of the present study; the differences in length may reflect differences in growth among various Lake Superior stocks.

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Genetic Control in the Lakeward Migrations of Sockeye Salmon (*Oncorhynchus nerka*) Fry[1]

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ABSTRACT

Eggs of sockeye salmon taken from tributary, outlet, and beach spawners at Karluk, Alaska, were treated identically from time of egg fertilization through time of testing as fry in a laboratory. Test lots were released during the day and at night in a central release pool from which the fry could migrate either upstream or downstream through simulated stream channels. Oxygen-saturated water at 50 F (10 C) was pumped through the 40-ft (12.2-m) gravel-bottomed simulated stream at about 0.3 ft/sec (9.1 cm/sec).

Test results showed that directions (upstream or downstream) and times (day or night) of migration differed substantially between fry from the tributary and those from the outlet. Fry from beach spawning reacted in a manner similar to that of the tributary fry. These differences were concluded to be of genetic origin. The possible interaction of innate behavior and environment in controlling the migratory movements of salmonid fry is discussed along with the significance of choosing a donor stock with appropriate innate responses to make best use of a new environment.

INTRODUCTION

Lake-resident populations of salmonids often spawn in both tributary and outlet streams. Although the means and precision of homing to natal streams have been studied (Hasler and Wisby, 1951; Cope, 1957; Stuart, 1957; Lindsey et al., 1959; Hartman and Raleigh, 1964), the mechanisms by which the progeny are brought into the lake-rearing areas have received little attention. Obviously, fry from outlet streams and fry from tributary streams must differ in their response to currents if both groups enter the lake.

For fry of rainbow trout (*Salmo gairdneri*) from inlet and outlet streams at Loon Lake, British Columbia, Northcote (1962) postulated: "(1) *genetically distinct* outlet and inlet stocks each maintaining appropriate innate behavior responses which result in movement of young into the lake; (2) *genetically similar* outlet and inlet stocks responding to environmental differences between the streams which produce appropriate current responses and other behavior characteristics resulting in movement of young into the lake." A third explanation also appears possible: (3) *genetically distinct* outlet and inlet demes maintaining innate behavior responses which may be modified by the environment.

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Primarily on a theoretical basis, Lindsey et al. (1959) rejected the possibility of genetically distinct demes of rainbow trout at Loon Lake. Northcote (1962) thus centered his investigation on the effects of the environment. He concluded: "Differences in water temperature between Outlet and Inlet Creeks regulate differences in direction of migration through action on behavior associated with downstream movement, maintenance of position, and upstream movement." He found that fry moved downstream in cooler water, but upstream in warmer water and with sharp rises in water temperature.

In applying Northcote's findings to other species and field situations, I observed that emergent fry of sockeye salmon at Karluk Lake, Alaska, moved upstream at temperatures well below those published by Northcote; this movement did not necessarily accompany sharp increases in temperature. Also, sympatric demes of stream-spawning cutthroat trout (*Salmo clarki*) occur in certain tributaries to the St. Joe River in northern Idaho (Averett, 1962; MacPhee, 1966). Progeny of adfluvial cutthroat trout move downstream to the lake to feed and grow, whereas the progeny of upstream fluvial spawners remain in the stream. The same tributary may contain demes of cutthroat trout that maintain themselves above impassable falls. A persistent downstream migration of these fry under any environmental condition would eventually eliminate these demes. The rather similar environmental conditions encountered by all three demes of fry and their different reactions suggested behavior patterns under genetic rather than environmental control.

I theorized that fry migrating in the "wrong" direction in either a tributary or outlet stream could conceivably fail to survive and maintain the race. Fry emerging from a lake beach, however, would not be subject to the same forces of natural selection. Both upstream- and downstream-migrating individuals might be found within this group; it might be the gene pool from which the tributary and outlet demes originated. Loyd A. Royal stated (personal communication, 1965) that E. L. Brannon, of the International Pacific Salmon Fisheries Commission, found that emerging sockeye salmon fry gathered at the upstream end of a hatching trough if they came from a deme spawning below the lake, but that those from a lake tributary tended to collect at the downstream end of the trough. Fry from beach spawning at Cultus Lake tended to disperse without any consistent orientation. This behavior led me to include fry spawned in beach areas in the preliminary tests.

During the winter of 1965–66, I conducted laboratory tests with sockeye salmon fry from tributary and outlet streams of Karluk Lake, and from the lake beach, to test the null hypothesis that innate behavior did not control lake-oriented migrations of salmonid fry. I reasoned that if handling and environment were kept identical for "pure" demes of outlet, tributary, and beach fry, any significant differences in their lakeward migration would then be attributable to genetic differences.

METHODS AND MATERIALS

A "U"-shaped trough (Fig. 1) was constructed of plywood and sealed with fiberglass resin. It consisted of a central release pool that opened at each end into a simulated stream channel. Each channel contained a small resting pool, which in turn opened into a second section of stream channels that doubled back alongside the first. These channels emptied into trapping pools. Oxygen-saturated water at 50 F (10 C) was pumped into the trough through a baffled plastic screen gate and circulated through the system as shown in Fig. 1. Two inches (5.08 cm) of water flowed over 1 inch (2.54 cm) of gravel through the stream sections. Water depths in the release pool and each of the two resting pools were 14.0 inches (35.6 cm) and 10.5 inches (26.7 cm), respectively. Water velocity of about 0.3 ft/sec (9.1 cm/sec) was maintained through the stream channels.

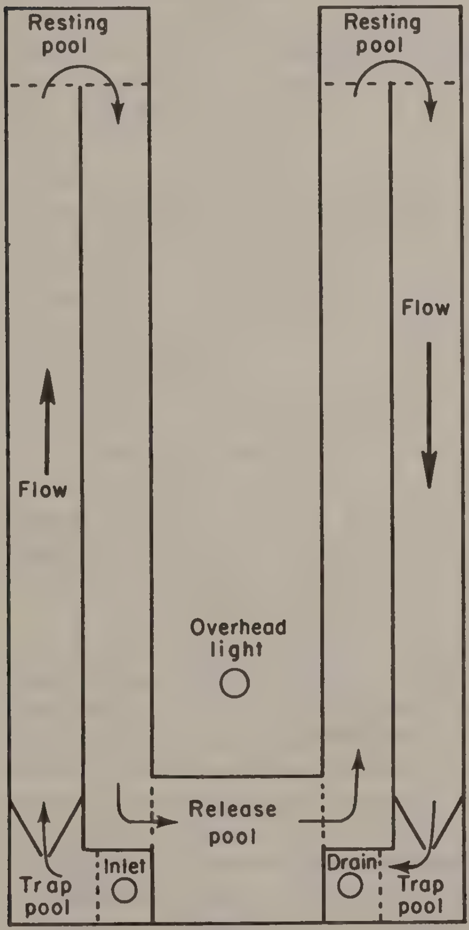
Resting pool
Resting pool
Flow
Flow
Overhead light
Release pool
Inlet
Drain
Trap pool
Trap pool

FIG. 1. *Left*, plan view of trough used for testing the innate response of sockeye salmon fry to a current. Arrows show direction of water flow.

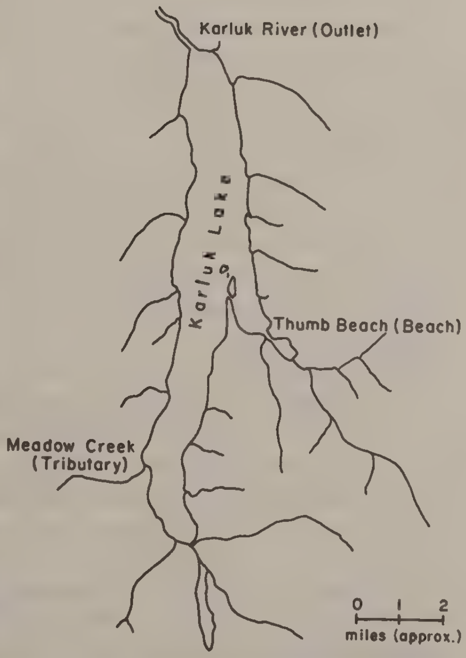
Karluk River (Outlet)
Karluk Lake
Thumb Beach (Beach)
Meadow Creek (Tributary)
0 1 2
miles (approx.)

FIG. 2. *Right*, spawning areas of the three donor demes of sockeye salmon at Karluk Lake on the northwestern part of Kodiak Island, Alaska.

The entire system was enclosed with black plastic sheeting to seal out exterior light. It was illuminated by a 60-w light bulb connected to an automated lighting system that simulated the gradual rising and setting of the sun and produced a day length of about 11 hr.

Eggs from three widely separated spawning areas of the Karluk Lake populations of sockeye salmon were selected for the study: Meadow Creek, a tributary to upper Karluk Lake; Thumb Beach, midway up the lake; and Karluk River at the lake outlet (Fig. 2). Hartman and Raleigh (1964) found that tributary homing of sockeye salmon at Karluk Lake ensured genetic separation. Eggs were collected on September 6, 1965, from each of the three groups of spawners; only fish actually engaged in spawning were taken. The eggs were fertilized and allowed to water-harden for 2 hr. They were then placed in plastic foam drip-type shipping containers, iced, and sent by airfreight to a fish hatchery at Lewiston, Idaho. The total time between taking eggs and putting them in hatchery trays at Lewiston late on September 6 was 15 hr.

Water at Lewiston hatchery is supplied by springs at a stable temperature of 50–52 F (10.0–11.1 C). Hatching was virtually completed by November 20 for the outlet deme, and by November 23 for the tributary and beach demes. The yolk sacs were absorbed by mid-December; the fish were then transferred 45 miles (72.4 km) for testing at the Small Animal Laboratory, University of Idaho, at Moscow, Idaho. The water temperature of the holding tank at the laboratory was maintained at 44–46 F (6.7–7.8 C). Test lots were transferred to water of 50 F (10 C) in an acclimation tank 48–72 hr before testing. Twenty-four hours before testing, two lots of 100 fish each were transferred to the test trough and held under test light levels and water conditions.

Paired releases of different combinations of fry originating from tributary, outlet, or beach spawning areas were made for each test. To distinguish between lots, one lot in each test was stained lightly with Bismark Brown Y dye (Deacon, 1961).[3] The test was repeated the following day, but the opposite group received the stain.

Both lots were released simultaneously in the central release pool of the trough and were free to move upstream or downstream. Both traps at the end of the test facility were emptied hourly. Fish removed from the traps were tallied by deme origin and by the direction and time of migration; they were then discarded. An individual test was considered completed when (1) all of the fish had entered the traps or (2) 90% of the fish had migrated within 24 hr from time of release.

To test the effect of time of release on migration I made releases at 0200, 0600, 1000, 1400, 1800, and 2200 hr. Three of the release periods were during darkness and three during daylight. Precautions were taken at all times to give identical treatment to both lots of fish in a test series.

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[3] The concentrations of stain (1:40,000) were weaker and exposure times (3 hr) shorter than those given by Deacon.

MOVEMENTS OF FRY

The first series of tests included all three demes of fry — tributary, outlet, and beach. The time and direction of migration of the Thumb beach fry did not differ significantly from those of the tributary fry. These results contrasted with the observations of E. L. Brannon cited earlier. But Thumb beach spawning is continuous with Lower Thumb tributary spawning at Karluk Lake, whereas no tributary spawning occurs at Cultus Lake. In the present study, samples taken from the Karluk Lake fry 1 month after hatching indicated a closer relation between the lengths of tributary and beach fry than between lengths of beach and outlet fry (Table I). Lengths of the tributary fry were not significantly different from those of the beach fry ($P > .50$); lengths of both tributary and beach fry differed from those of the outlet fry ($P < .01$).

Table I. Length frequencies of sockeye salmon fry from representative samples of different origin.

Fork length (*mm*)	Origin of fry Tributary	Beach	Outlet
26	5	3	–
27	5	5	–
28	10	11	1
29	6	9	4
30	3	2	12
31	1	–	7
32	–	–	6
Avg length	28.0	28.1	30.4

Because of the similarities in incubation time (noted earlier), migration, length distribution, and the proximity of spawning, the Thumb beach fry were assumed to be genetically similar to the tributary fry and were not tested further.

The primary purpose of the tests was to compare directions of migration between outlet and tributary fry, and to examine the effect of light and release time on time of migration. Three major differences were found in the migratory patterns of the two demes (Tables II and III).

In the time allotted for the test, 98% of the tributary fry moved downstream, 1% moved upstream, and 1% did not enter the traps. The corresponding values for the outlet fry were 66%, 30%, and 4%. The direction of movement thus differed significantly between demes. The percentage of tributary fry that moved upstream and the percentages of both groups that did not move were negligible.

TABLE II. Cumulative counts of sockeye salmon fry in traps, from paired releases of 100-fish test lots; fish in one lot of each release were stained.

Release time (*hr*) and group stained, each release	Outlet fry					Tributary fry				
	Movement					Movement				
	Upstream		Downstream			Upstream		Downstream		
	Day	Night	Day	Night	Not trapped	Day	Night	Day	Night	Not trapped
0200 Outlet	30	12	21	35	2	0	2	1	96	1
Tributary	16	25	14	41	4	0	6	2	90	2
0600 Outlet	12	32	8	45	3	0	0	1	99	0
Tributary	5	24	7	57	7	0	0	1	98	1
1000 Tributary	28	2	59	11	0	0	0	1	99	0
Outlet	28	0	11	55	6	0	0	16	82	2
1400 Tributary	8	2	50	38	2	0	0	20	80	0
Outlet	7	0	47	44	2	1	0	18	81	0
1800 Tributary	36	9	47	8	0	0	0	8	92	0
Outlet	14	23	49	11	3	0	0	1	97	2
2200 Tributary	1	21	7	61	10	1	0	0	98	1
Outlet	1	21	4	63	11	0	3	1	94	2
Total:	186	171	324	469	50	2	11	70	1106	11
Percentages:	15.50	14.25	27.0	39.08	4.17	0.17	0.92	5.83	92.17	0.92
	29.75		66.08			1.09		98.00		
	Day 42.50		Night 53.33			Day 6.00		Night 93.09		

TABLE III. Summary of pertinent results from analysis of variance of data in Table II.

Source to	Outlet fry, significance at 0.01	Tributary fry, significance at 0.01
Direction	S.	S.
Light condition	N.S.	S.
Direction × light	N.S.	S.
Light × release time	S.	N.S.

Only 6% of the tributary fry moved into the traps during daytime, whereas 93% moved at night; however, 42.5% of the outlet fry moved into traps during the day and 53.0% at night. Presence or absence of light did not significantly affect the time of movement of the outlet fry, but did affect that of the tributary fry (Table II). Hourly catch records confirmed that the fish started to move on the day or night after release. Most movements of tributary fish occurred during the first 2 hr of darkness. The interaction between release time and light condition confirmed that outlet fry migrated both day and night according to time of release, but that nearly all tributary fry migrated at night regardless of when they were released.

The staining process used to distinguish between test lots had no detectable effect on migration.

The tests demonstrated that the outlet and tributary fry differed significantly in their direction of migration and time of movement. Because handling was identical, these differences evidently were innate. The null hypothesis stated earlier was therefore rejected.

POSSIBLE EFFECT OF LENGTH DIFFERENCES

The tributary fry were 2 mm shorter in average fork length than the outlet fry (Table I). The question arises of the possible effect of this difference in size on the success of upstream movement and consequently on the results of the test.

Information on the swimming ability of salmonid fry 32 mm or less in length is limited. Kerr (1953) found that wild juvenile chinook salmon (*O. tshawytscha*) 30–59 mm long could maintain position in a test flume for 10-min exposures in velocities between 1.0 and 1.5 ft/sec (30.48 and 45.72 cm/sec) and for 1 hr at velocities of 1.0–1.2 ft/sec (30.48–36.58 cm/sec). These wild chinook salmon fry thus withstood velocities 3–5 times higher than the smaller sockeye salmon fry in the present tests. I do not believe the swimming ability of sockeye salmon fry is so much poorer than that of chinook salmon fry that it was a significant factor in the low velocity (9.1 cm/sec) of the present tests.

Measurements indicated that about two-thirds of the tributary fry were within the length range of the outlet fry (Table I). Even if length were a controlling factor in upstream migration, one would expect a much higher percentage of upstream movement by tributary fry than was actually recorded. Length cannot be entirely eliminated as a limiting factor on upstream movement, but I do not consider it of consequence in the present tests because it can hardly account for the consistent and significant separations attained.

RELATION OF TEST RESULTS TO MIGRATION AT KARLUK LAKE

The proportion of fry from tributary or outlet demes moving upstream or downstream during the tests should not be construed as an accurate estimate of natural migration in either direction. The experimental trough was only 40 ft (12.2 m) long and a fish that strayed 20 ft (6.1 m) in either direction from the central release pool was trapped and removed. The salient feature of the laboratory test is that even within this short distance, fry from the two demes consistently and significantly differed in patterns of migration.

Table IV, which shows the results of a limited fry-trapping study at the outlet of Karluk Lake in 1958, is perhaps more indicative of natural movements of fry in the stream than are laboratory tests.

TABLE IV. Routes and direction of migration of sockeye salmon fry in the Karluk River in 1958.[a]

Date	Trapping site and distance from bank	Upstream catch/hr	Downstream catch/hr
April 12–14	East bank, 0–3 ft (0.0–2.7 m)	71.4	2.2
8–11	" 3–6 ft (2.7–5.5 m)	13.9	8.9
8–11	Midstream	0.5[b]	1.8
23–26	"	0.2[b]	3.5
18–19	West bank, 0–3 ft (0.0–2.7 m)	177.0	8.4

[a] The fry migration up Karluk River into the lake in 1958 was almost completed by late May. In diminishing numbers, however, a few young of the year were still moving upstream until August when the last visual observation was made. These stragglers may represent the upstream migration of a portion of those fry swept downstream by the current or may represent a group of fry that normally spend a growing period in the river.

[b] Fry captured moving upstream in midstream were probably able to do so only because the trap created an area of relatively quiet water immediately below it.

POSSIBLE MECHANISMS THAT CONTROL MIGRATION

That fish are sensitive to changes in temperature is well documented. Bardach and Bjorklund (1957) found the level of temperature discrimination to be about .05 C or less. Salmonids apparently tend to move upstream toward the headwaters and tributaries to avoid temperatures that rise above the preferred range. Likewise, they tend to move downstream out of some tributaries into deeper water to avoid extremely low temperatures during winter. High or low temperatures could elicit these responses in emergent salmonid fry, therefore, as observed in rainbow trout fry in Loon Lake by Northcote (1962) and thus affect their lakeward migrations as postulated in Fig. 3. The differences in temperature between outlet and tributary streams (as discussed by Northcote, 1962) would tend to increase or to reinforce the inherent patterns of lakeward migration, but temperature extremes may eventually override the inherent patterns.

The controlling stimuli may possibly vary between species and environments: i.e., temperature at Loon Lake, innate behavior at Karluk Lake. Young salmonids may receive other directional stimuli as well as those already found. For example, the lake may contribute an attracting substance into the outlet stream that is absent in the tributaries; or the presence of lake food organisms in the outlet stream may attract the outlet fry upstream. It is postulated that the ultimate direction of migration is determined by the summation of both extrinsic and intrinsic stimuli.

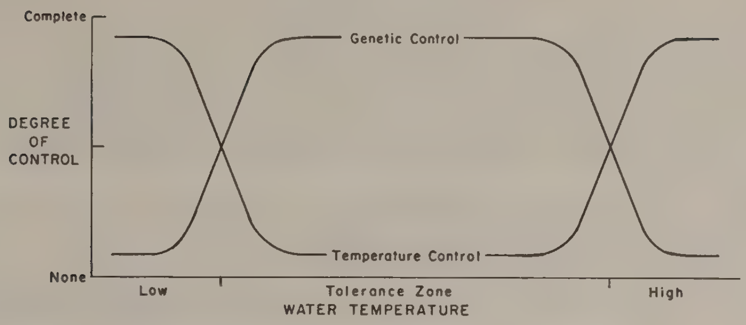

FIG. 3. Theoretical interaction between temperature and genetics in controlling the direction of migration of salmonid fry.

From time to time attempts are made with variable success to establish stocks of fish in new areas or to bolster depleted stocks by transplants of eggs or fry. A. M. R. Burnet (personal communication, 1966) planted rainbow trout eggs from a lake population into a New Zealand stream; downstream movement of fry and fingerlings was later observed at a fish trap. The trapped fry made up 5% of the number of eggs planted, and there was no evidence of the establishment of a resident population. Later, when eggs from a stream population were planted, no downstream migration of fry or fingerlings was observed, and a population was established in the stream.

Attention has been focused recently on the importance of matching the characteristics of the donor population to the requirements of the environment to be seeded. There is now reason to believe that inherent migration tendencies of emergent fry may significantly influence the success or failure of a planting attempt and must be considered in the selection of an exotic stock for an area. Obviously, either tributary or outlet populations could meet the requirements if environment alone controlled the migration. But when innate migration patterns are involved, plantings are more likely to succeed if the innate behavior as well as the environment of the donor is matched to the new environment.

SUMMARY AND CONCLUSIONS

1. During the winter of 1965–66 the response to current of outlet, tributary, and beach demes of sockeye salmon fry from Karluk Lake, Alaska, were tested in a laboratory. Handling and environment were identical from time of egg fertilization through testing.

2. The test results demonstrated that outlet and tributary fry differed significantly in their direction and time of migration. Because the environment was kept identical these differences were concluded to be of genetic origin.

3. The results of my study together with those of a study by Northcote (1962) on rainbow trout imply that the direction of migration of salmonid fry may be caused by: (*a*) environmental control (Northcote, 1962); (*b*) innate behavior (present study); or (*c*) a combination of intrinsic and extrinsic factors.

4. Innate patterns of migratory behavior may significantly affect the success of an egg or fry transplant and therefore should be considered in choosing a stock of fish for planting in a new environment.

ACKNOWLEDGMENTS

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The constructive criticisms of Drs Craig MacPhee and Donald Chapman of the University of Idaho contributed substantially to the study. Dr Dale Everson of the University of Idaho and Mr William Davis of the Bureau of Commercial Fisheries gave advice and assistance on the statistical analysis.

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15

Cetaceans

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Cetaceans in General

All cetaceans are exclusively aquatic and may be characterized as follows: body fusiform; anterior limbs (flippers) paddle-shaped (joints distal to shoulder immobile); no external digits or claws; no external hind limbs; tail flattened laterally and bearing horizontal flukes at the tip (with the possible exception of family *Basilosauridae—see Howell, 1930: 198); only internal vestiges of the ear pinna present; body essentially hairless; no sebaceous glands; thick subcutaneous blubber layer.

Bones of skull strongly telescoped; external nares (blowhole) on the vertex (excepting in the Physeteridae and *Archaeoceti); rostrum greatly elongated; tympanoperiotic bones displaced ventrally and dissociated from adjacent bones of cranium; squamosal bearing a falciform process; basioccipital having crests which form a longitudinal arcade for accommodation of larynx and nasopharyngeal muscle complex; pterygoid enlarged, overriding and intruding into palatine; pterygoid split into lateral and mesial laminae; zygomatic process excavated to form the tympanosquamosal recess; accessory air-sinuses present in the region of the middle ear; no clavicle; ribs of 9 to 18 pairs; pelvic girdle vestigial, not attached to vertebral column; sacral vertebrae separate.

Lungs not lobed; diaphragm oblique; *retia mirabilia* greatly developed in thoracic and basicranial regions; liver not lobed; no gall bladder; stomach having four or more chambers; each kidney divided into separate lobes; testes permanently abdominal; penis retractile; uterus bipartite; placenta epitheliochorial (diffuse, nondeciduate); urethral and vaginal orifices separate; single pair of mammae, "inguinal" in position, and surrounded by the *m. compressor mammae,* a specialized part of the *m. panniculus carnosus;* teats in bottom of deep grooves, extruded during nursing.

Cetaceans, when adult, vary in size from a length of about 1.3 m. and a weight of about 30 kg., to over 30 m. and 160,000 kg. The larger species are the largest known animals, living or fossil.

The origin of whales is unknown beyond the fact that they are unquestionably placental mammals. Probably they separated from the primitive eutherian stock during the Cretaceous, prior to or simultaneously with the differentiation of the other modern orders. The ancestral cetaceans were possibly inhabitants of freshwater lakes and streams. Palaeontological and anatomical data reveal an ancient, basic separation into three distinct phyletic lines—the toothed whales, Odontoceti, the baleen whales, Mysticeti, and the extinct zeuglodonts, Archaeoceti (or Zeuglodontia). These three taxa have customarily been ranked as suborders under the single order Cetacea. No known forms bridge the gaps between them; no fossils belonging to any one of them could have been ancestral to either of the other. Almost all students of cetacean phylogeny have raised the question of the possibility of a polyphyletic origin. Most of the morphological similarities between the three taxa may be interpreted either as retention of primitive eutherian characters, or as parallel adaptations to a pelagic life. Many are shared with the sirenians and pinnipeds. Present knowledge neither proves a monophyletic origin for the Cetacea, nor provides evidence incompatible with such a hypothesis. However, the differences between the three taxa are greater than those between many universally recognized orders of mammals (for example, the Artiodactyla and Perissodactyla, which Simpson even places in separate superorders). Recently, the consensus has been shifting in favor of ordinal rank for each of the three groups. This arrangement is followed here.

Cetaceans are the swiftest animals in the sea. Dolphins can maintain a sustained speed of 26 to 33 km. per hour (Johannessen and Harder, 1960). The large rorquals can attain speeds of about 37 km. per hour for short periods; their maximum sustained speed is about 28 km. per hour, but normally they do not exceed 12 km. per hour. Cetaceans swim by oscillating the tail and flukes in a vertical plane; the flippers usually function only as stabilizers. The smaller species probably achieve nearly full laminar flow, as they can swim much faster than is predictable on the basis of muscle power and drag under turbulent flow.

Respiration in cetaceans is characterized by brief periods of eupnea alternating with periods of apnea varying from 15 seconds to 2 hours. The lungs of cetaceans, compared with those of terrestrial mammals, show a greater rigidity and elasticity because of increased cartilaginous support. In the baleen whales, sperm whales, and bottle-nosed whales the septa projecting into the proximal portion of the air sacs contain heavy myoelastic bundles. In the smaller toothed whales these bundles are atrophied, but there is a series of myoelastic sphincters in the smallest bronchioles. In both the bundles and the sphincters, the muscular part could act to close the air sacs, while the elastic part could facilitate rapid expiration. The presence of two layers of capillaries in the interalveolar septa facilitates rapid gaseous exchange. The relative lung capacity in dolphins and porpoises is almost one and a half times that of terrestrial mammals, but in the rorquals and deep-diving toothed whales it is only half; the ratio of residual air to tidal air is very low—about 10 to 20 per cent. Eight to 12 per cent of the oxygen in inhaled air is utilized, compared with about 4 per cent in terrestrial mammals. (Wislocki and Belanger, 1940.)

The ratio of volume of blood to volume of body and the oxygen storage capacity of the hemoglobin do not differ significantly from that ratio and capacity in terrestrial mammals, but there are 7 to 11 million erythrocytes per cubic millimeter of blood, or as much as twice the average number in most terrestrial mammals. The myoglobin content of the muscles of cetaceans is 9 to 44 gm. per kg., or about two to nine times as much as in terrestrial mammals—in fact the meat of the deep-diving sperm and bottle-nosed whales is almost black. Oxygen stores in tissue fluids are the same as in nondiving mammals. The principal adaptations to prolonged diving involve (1) anaerobic glycolysis, (2) tolerance to high levels of lactic acid, and (3) a relative insensitivity to carbon dioxide. During submersion, the *retia mirabilia* possibly function as arteriovenous shunts, permitting the blood to bypass the muscles. Bradycardia during diving is apparently not as marked as in pinnipeds. In *Tursiops truncatus* the heart rate drops from 110 beats per minute while at the surface, to about 50 while submerged. In *Phocoena phocoena* it drops from 115–120 per minute to 50–60 per minute. The larger species have much slower pulse rates. *Orcinus orca* has a rate of about 60 beats per minute at the surface, 30 per minute while submerged. The modal rate in *Delphinapterus leucas* while submerged is 16 to 17 per minute. Heart rate in a moribund stranded *Balaenoptera physalus* was 27 per minute; the normal rate may be about 10 per minute (Irving *et al.*, 1941; Kanwisher and Sundnes, 1965).

Some species of whales dive to depths of over 1000 meters, where they are subject to pressures in excess of 100 atmospheres. When deeper than about 100 meters, the pressure collapses the pulmonary alveoli, compressing the air into the bronchi, trachea, nasal passages, and accessory air sacs, thus preventing nitrogen absorption through the alveolar membrane. Excess nitrogen may be absorbed by the emulsified mucous-oil foam contained in the air sinuses, which is expelled during exhalation, forming the characteristic "blow" (Scholander, 1940; Harrison and Tomlinson, 1963).

In sea water near freezing temperature (−2° C.), cetaceans experience the greatest cooling effect encountered by mammals. In such an extreme environment, the smaller species such as *Phocoena phocoena* can maintain their normal body temperature of about 35° C. because their metabolic rate (*ca.* 3500 kcal. per 24 hr.) is about three times that of terrestrial mammals of the same weight. Heat loss is reduced by arteriovenous counter-current heat exchange in the flippers and flukes, and by cooling of the skin and the thick blubber layer, which may constitute over 40 per cent of the body weight in *Phocoena phocoena.* The larger whales, because of their low surface-to-volume ratio, have no problem in keeping warm. During strong exertion, or while in warmer waters, heat loss is facilitated by increased blood flow through the superficial veins of the flippers and flukes (Irving and Hart, 1957; Scholander and Schevill, 1955; Kanwisher and Sundnes, 1965).

Metabolic water seems to be the major source of moisture for cetaceans. Respiratory water loss of dolphins is much less than in terrestrial mammals of the same body weight. Those cetaceans which feed on fish, the blood and body fluids of which have a relatively low concentration of salt, do not face much of a problem in maintaining their salt balance. In the forms that feed on invertebrates, which are isotonic with sea water, osmotic regulation would appear to be more of a problem. However, the kidneys are capable of excreting a highly hypertonic urine, sufficient to maintain the balance (Krogh, 1939; Fetcher and Fetcher, 1942; Prosser, 1950; Coulombe *et al.*, 1965).

Cetaceans are the only animals other than elephants which have a brain larger than that of man. The weight of the brain varies from about 0.5 kg. in *Phocoena phocoena* to 9.2 kg. in *Physeter catodon.* However, the ratio of brain weight to body weight is low, varying from 0.8 per cent in *P. phocoena* to 0.007 per cent in *Balaenoptera musculus.* The surface of the cetacean brain is highly convoluted. In captivity, the smaller odontocetes have revealed a high level of intelligence, superior to that of dogs. These odontocetes are readily tamed and trained, are playful, become affectionate toward man, and quickly learn games requiring superb agility and coordination.

Most cetaceans have eyes well adapted for underwater vision (Kellogg, 1928), but they also see well above water. *Platanista* is blind, *Lipotes* nearly so. Baleen whales have a tactile sense in sinus hairs (vibrissae) and in sensory tubercles on their tongue, lips, and palate (Nakai and Toshitomo, 1948; Ogawa and Toshitomo, 1950). The sense of smell is vestigial in mysticetes, absent in odontocetes. Vestiges (nonfunctional?) of the vomeronasal organs are found in the mysticetes. Whales have good directional hearing under water (Reysenbach de Haan, 1956; Fraser and Purves, 1960); they can detect ultrasonic frequencies up to 120 kc. (Schevill and Lawrence, 1953).

Many cetaceans—probably all odontocetes—employ echolocation (echo-ranging, or sonar) of the pulse-modulation type for navigation and food-finding. The most common phonations of odontocetes fall into two categories (which the animals can emit simultaneously): (1) clicks, or pings—pulses with a duration of 0.001 to 0.01 second, covering a broad band of frequencies from 100 to about 120,000 cycles per second, which are uttered in trains of five to several hundred per second; (2) whistles—frequency-modulated signals of about 0.5-second duration, with a very narrow frequency band of 4000 to 20,000 cycles per second. The clicks, which are produced in the nasal sac system, are used in echolocation. The whistles are apparently produced in the larynx, and are primarily communicative.

Recent experiments suggest that the concave shape of the dorsal surface of the skull functions as a sound reflecting surface, and that the fatty "melon" on the forehead serves as an acoustic lens, for directional beaming of the echolocation signals. These structures are notably well developed in those forms (e.g., *Physeter, Hyperoodon*) which regularly feed in the lightless bathypelagic zone, and those which live in turbid rivers (e.g., *Platanista,* which is blind).

The baleen whales produce a variety of moans and screams ranging from below 20 cycles per second to nearly 1000. The function of these phonations is probably communicative; mysticetes have not been shown to use echolocation (W. N. Kellogg, 1961; Norris *et al.,* 1961; Schevill and Watkins, 1962; Evans and Prescott, 1962; Schevill, 1964; Norris, 1964).

Most cetaceans are gregarious, and some species show a distinct social organization. *Orcinus orca* hunts cooperatively to kill large prey. Whales, particularly the odontocetes, have a large vocabulary of sounds which are apparently used in communication; cetacean "language" is currently being investigated (Lilly, 1962; Dreher and Evans, 1964).

The age at which cetaceans attain sexual maturity varies from 14 months in female *Phocoena* to more than 10 years in the larger mysticetes, in *Physeter,* and in male *Globicephala.* Cetaceans are seasonally monestrous, or show a strong tendency toward the monestrous condition. There is marked functional asymmetry of the ovaries in Delphinidae, Phocoenidae, and Monodontidae. All species are uniparous; multiple pregnancies occur in less than 1 per cent of cases, but there is no evidence that more than one young ever survives. Gestation periods range from 10 to 12 months in mysticetes, 11 to 16 months in odontocetes. The fetal growth rate (body length) is linear in odontocetes, but logarithmic during the last half of pregnancy in mysticetes. The weight of the newborn calf is about 3 or 4 per cent of that of the mother in the baleen whales, about 7 to 25 per cent in the toothed whales (being relatively larger in the smaller species). Parturition occurs in the water; breech presentation is normal, at least in odontocetes. The umbilical cord is short, and breaks at a weak spot close to the umbilicus after birth. The young are necessarily precocial, as they must be able to swim at birth. The milk is rich in fat and protein, low in lactose. The young grow rapidly, and are weaned at an age of from 4 months to 2 years (Eichelberger *et al.*, 1940; Slijper, 1956; Tavolga and Essapian, 1957; Laws, 1959; Ohsumi, 1964*b*).

Toothed whales feed on a wide variety of nektonic and benthic fishes and cephalopods; *Orcinus* also feeds on marine mammals and birds. Baleen whales are filter feeders, taking planktonic euphausiids, copepods, fishes, and pteropods, and (*Eschrichtius* only) benthic amphipods.

The endoparasites of cetaceans include cestodes, trematodes, nematodes, and acanthocephalans which infest the stomach, intestines, liver, urinogenital system, lungs, air sinuses, blubber, and fasciae between blubber and muscle. Consult Deliamure (1955) for a list of genera which normally occur in cetaceans.

Ectoparasites and epizoites of cetaceans include diatoms (chiefly *Cocconeis ceticola,* also including species of *Licmophora, Navicula, Gyrosigma, Stauroneis,* and *Plumosigma*) which may form an olive-colored film on the skin in colder waters (Hart, 1935; Nemoto, 1956, 1958). The sessile barnacles *Coronula, Cryptolepas, Tubicinella,* and *Xenobalanus* (Thoracica: Balanidae) grow on, or imbedded in, the skin. The stalked barnacles *Conchoderma auritum* and *C. virgatum* (Thoracica: Lepadidae) are hyperepizoites on *Coronula* and *Penella,* respectively. Whale-lice of the genera *Cyamus, Neocyamus, Platycyamus, Isocyamus,* and *Syncyamus* (Amphipoda: Cyamidae) live on the skin. The aberrant and highly specialized copepod *Penella* (Caligoida: Lernaeoceridae) grows "rooted" in the blubber. The lampreys *Petromyzon* and *Lampetra* (Hyperoartii: Petromyzontidae) often attack whales, and leave scars on the skin. The whalesucker *Remora australis* (Discocephali: Echineididae) attaches itself to cetaceans for transportation. The surfaces of the baleen plates of the mysticetes are inhabited by the copepod *Balaenophilus unisetus,* the nematode *Odontobius ceti,* and several genera of protozoans.

Important mortality factors under natural conditions are unknown. The only animal which regularly preys on cetaceans is the killer whale *Orcinus orca.* The occasional carnivorous individuals of the walrus *Odobenus rosmarus* rarely prey on the beluga *Delphinapterus leucas* and the narwhal *Monodon monoceros*. Remains of dolphins and porpoises have been found in the stomachs of tiger sharks *Galeocerdo cuvieri* and Greenland sharks *Somniosus microcephalus*. At the present time, the major predator of the larger whales is man, using the diesel-powered catcher boat with harpoon gun.

It is impossible to cite all of the publications consulted in the preparation of this account. A selection of the more important, mostly recent, papers on each subject is cited; through these the reader can trace the earlier literature. I have also used papers presented at the First International Symposium on Cetacean Research, Washington, D.C., 15–18 August 1963, although the proceedings (Norris, 1966) were published too late to attempt to cite individually any of the included papers. Useful general references are: Slijper's (1962) book on general biology; Scheffer and Rice's (1963) distributional list of the marine mammals of the world; Fraser's (in Norman and Fraser, 1948) and Kellogg's (1940) well-illustrated accounts, which include most of the world's species; Tomilin's (1957) treatise on the species occurring in the waters adjacent to the U.S.S.R.; Mackintosh's (1946) summary of the biology of the baleen whales; Beddard's (1900) book, which is outdated but still very useful; and Hershkovitz's (1966) nomenclatorial catalog of living species. For a review of the extinct *Archaeoceti, see Kellogg (1936). Howell's (1930) work on aquatic mammals contains much pertinent information. The best general account of the history of old-style and early modern whaling is the book by Jenkins (1921); also see the bibliography of the vast literature on this subject by Jenkins (1948). The history of modern whaling is treated in detail (in Norwegian) by Johnsen (1959; additional volumes in preparation by J. N. Tønnessen). For the technology of modern whaling, see Schubert (1955).

ORDER MYSTICETI

Diagnosis. Baleen present; teeth absent (vestigial dentition present in fetuses); skull symmetrical; maxillae with orbital plates; ascending processes of maxillae small and narrow, interlocking with frontals, not spreading over the expanded supraorbital processes; nasal bones forming anterior part of roof of narial passages; narial openings paired, narial passages simple, closed by one pair of plugs; respiratory and alimentary tracts not permanently separated, laryngeal cartilages not forming a tube; internal nares closed by epiglottis during swallowing; pharynx closed by oro-pharyngeal sphincter during breathing; cartilaginous tracheal rings open; mandibular symphysis ligamentous; ribs single-headed, no sternal ribs; sternum consisting of a single bone, articulating only with the anterior pair of ribs.

Recent Distribution. All oceans and contiguous seas.

Geologic Range. Middle Oligocene to Recent.

Families. (4, 5 Recent genera, 10 Recent species)

*Cetotheriidae
Balaenidae
Eschrichtiidae
Balaenopteridae

Remarks. The classification of the Mysticeti has been discussed by Winge (1921), Miller (1923), Kellogg (1928), Slijper (1936), and Fraser and Purves (1960).

FAMILY BALAENIDAE Gray, 1825
Right whales

Diagnosis. Posterior border of nasals and premaxillae anterior to supraorbital processes of the frontals; maxillae without nasal processes; nasals reduced; frontals scarcely exposed on vertex; anterior border of parietals behind posterior border of premaxillae, maxillae, and nasals; supraoccipital extending forward beyond level of zygomatic processes of squamosal; rostrum narrow and highly arched; mandible not conspicuously bowed outward; cervical vertebrae fused; throat not grooved; tongue heavy and muscular; baleen plates long, narrow, left and right baleen rows separated anteriorly.

General Characters. Body proportions robust; dorsal fin absent in *Balaena,* falcate in *Caperea;* length of head about 28 per cent to 33 per cent total length in *Balaena;* adult length 6.1 to 6.4 m. in *Caperea,* to 17.6 m. in *Balaena mysticetus,* and to 18.3 m. in *B. glacialis;* weight of a *B. glacialis* (17.1 m.) was 67,197 kg.; females larger than males; color dark gray to black (white patches on chin of *B. mysticetus*); *B. glacialis* with calloused "bonnet" on top of snout, and a row of small callosities on either side of the lower jaw.

Caperea has 17 pairs of broad, flat ribs (but none on the first dorsal vertebra). In adult males of *Balaena glacialis,* the testes are enormous, sometimes weighing over 900 kg. each!

Habits. In the Northern Hemisphere, the large right whales, *Balaena,* feed primarily on "brit," minute orange calanoid copepods (e.g., *Calanus finmarchicus*) the bowhead, *B. mysticetus,* is also alleged to take pteropods (*Clione* and *Limacina*). In the Southern Hemisphere, black right whales, *B. glacialis,* feed primarily on "lobster-krill" (also called "brit"), the post-larvae of a decapod crustacean (*Munida gregaria*). Right whales are only moderately migratory, and remain in high-latitude temperate waters during the winter; bowheads remain near the ice-edge. According to the Alaskan Eskimos, the bowhead is capable of breaking its way up through ice almost a meter thick. Little is known concerning reproduction and the age at sexual maturity is not known. Young are born in late winter (January to April) in the Northern Hemisphere after gestation lasting probably about 12 months. Calves are said to be weaned at about 12 months of age. Female bowheads apparently breed in alternate years.

Right whales are not gregarious, and usually occur singly or in small groups. Almost nothing is known of the habits of the rare pygmy right whale, *Caperea marginata;* its unique skeletal structure suggests that it may spend much time lying on the bottom. Because of their slowness, buoyant carcasses, high oil yield, and long pliant baleen, the large right whales were ruthlessly exploited in the past; they are now rare, but increasing in numbers, and are completely protected from commercial whaling operations under the International Convention for the Regulation of Whaling. Alaskan Eskimos regularly hunt the bowhead from camps on the edge of the fast ice, using skin boats, darting guns, and bomb-lances (Davies and Guiler, 1957; Omura, 1958; Klumov, 1962).

Habitat. Oceanic or neritic, chiefly in coastal areas; *Balaena mysticetus* remains in or near pack-ice.

Recent Distribution. All oceans, except tropical and south polar seas.

Recent Genera. (2, 3 Recent species)

Balaena Linnaeus, 1758 (2) [including *Eubalaena* Gray, 1864]
Caperea Gray, 1864 (1) [= *Neobalaena* Gray, 1870]

Geologic Range. Early Miocene to Pleistocene in South America; early Pliocene to Pleistocene in Europe; Recent in all oceans.

Major Fossil Groups. Four extinct genera of Balaeninae.

Remarks. Miller (1923) and Kellogg (1928) placed *Caperea* in a separate family, "Neobalaenidae." Slijper (1936), Simpson (1945*a*), and Fraser and Purves (1960) placed it in the family Balaenidae, and did not recognize subfamilies.

FAMILY ESCHRICHTIIDAE Ellerman and Morrison-Scott, 1951
Gray whale

Diagnosis. Nasals and nasal processes of premaxillae extending backward beyond level of anterior border of supraorbital processes of frontals; maxillae with nasal processes; nasals large; frontals broadly exposed on vertex; anterior border of parietals behind posterior border of premaxillae, maxillae, and nasals; supraoccipital not extending forward beyond level of zygomatic processes of squamosal; rostrum narrow and

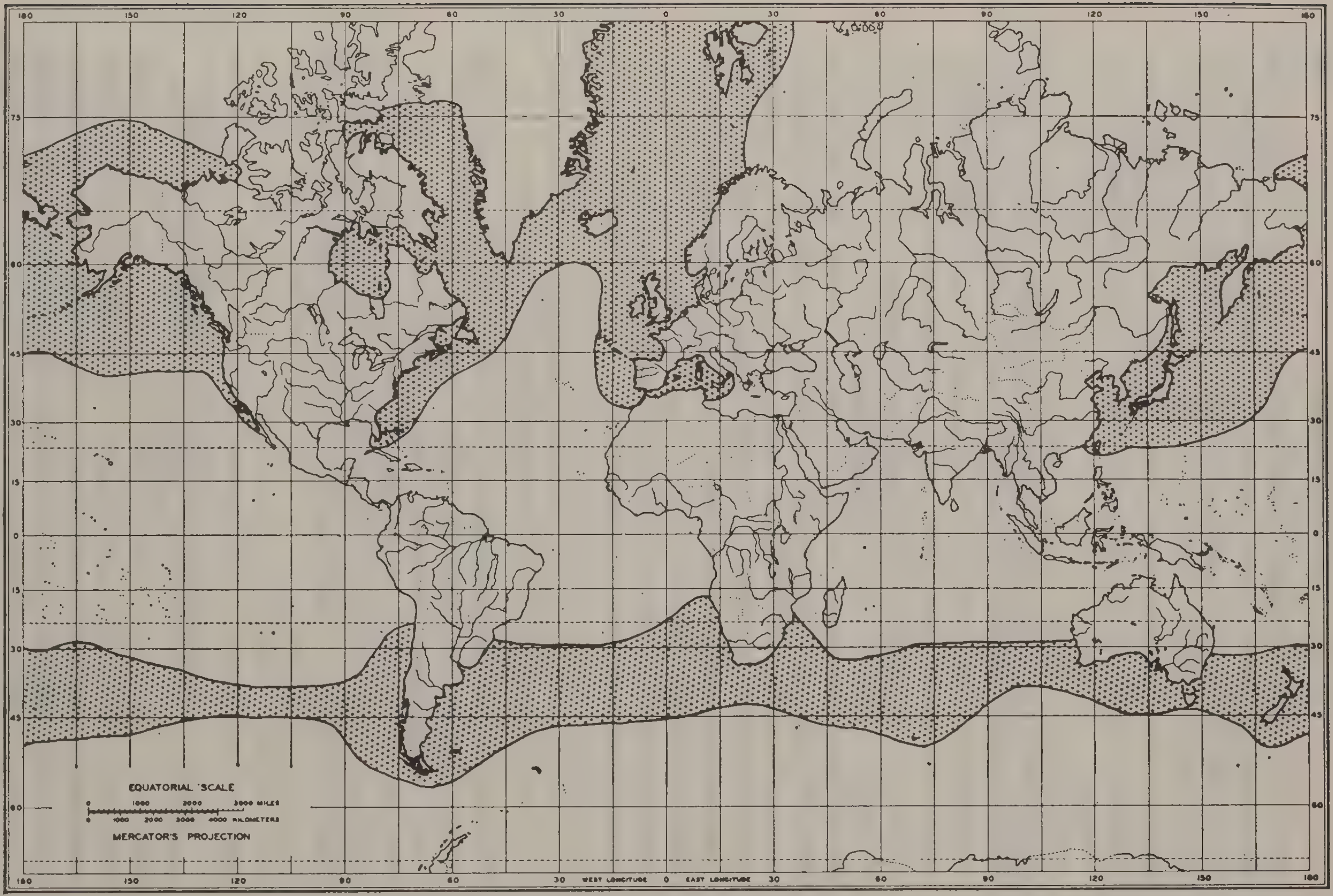

EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE

Fig. 45. Distribution of Balaenidae.

arched; mandible not conspicuously bowed outward; cervical vertebrae separate; throat with two (rarely three or four) short grooves; tongue heavy and muscular; baleen plates short, narrow; left and right baleen rows separated anteriorly.

General Characters. Body slender, snout blunt; no dorsal fin, low dorsal hump, crenulate dorsal ridge on tail; length of sexually mature adult females 12.1 to 14.9 m.; of males, 10.9 to 13.1 m.; weight of a female (13.3 m.) was 31,466 kg.; color gray with white mottling. Most if not all individuals have a thick-walled, fluid-filled, cystlike structure, 10 to 25 cm. in diameter, on the ventral surface of the caudal peduncle between the blubber and the muscles.

Habits. Most gray whales *Eschrichtius gibbosus* spend the summer in the shallow coastal waters of the Chukchi, Bering, and Okhotsk seas. They feed on benthic amphipods which they obtain by stirring up the silty bottom sediments with their snouts. In late autumn they migrate southward 5000 to 11,000 km., the longest migration of any mammal, closely following the shoreline most of the way; in spring they follow much the same course northward. They fast during most of the time they are migrating and on their wintering grounds. They are judged to attain sexual maturity at an age of 8 to 9 years, based on the assumption that one ear plug lamination is formed each year (see discussion under *Remarks* in the account of Balaenopteridae). Calves are born in January and February in certain nearly landlocked lagoons and bays in Baja California and Korea. Gestation requires about 12 months. Females do not bear calves two years in succession. During migration, gray whales travel singly or in pods of up to a dozen. On the arctic feeding grounds, loose groups of up to 150 individuals have been seen. Gray whales usually remain submerged for about 4 minutes, then surface and blow five or six times; they raise their flukes high in the air as they sound almost vertically. Normal swimming speed on migration is 7 to 10 km. per hour. Conspicuous behaviorisms are "breaching," "finning," and "spy-hopping."

In the years from 1853 to 1856, the California (east Pacific) population was estimated at nearly 30,000. Gray whales were nearly exterminated between 1850 and 1925; under complete protection from commercial whaling by the International Convention for the Regulation of Whaling, they have greatly increased. A few are killed by the Alaskan Eskimos. In the winter of 1959–1960, the California population numbered about 6000, and it is increasing about 10 per cent annually. The annual migration of the gray whale is one of the outstanding wildlife spectacles in North America, and is viewed by almost one million visitors annually at the Cabrillo National Monument on Point Loma above San Diego Bay (Gilmore, 1960; Pike, 1962).

Habitat. Neritic, estuarine during breeding season.

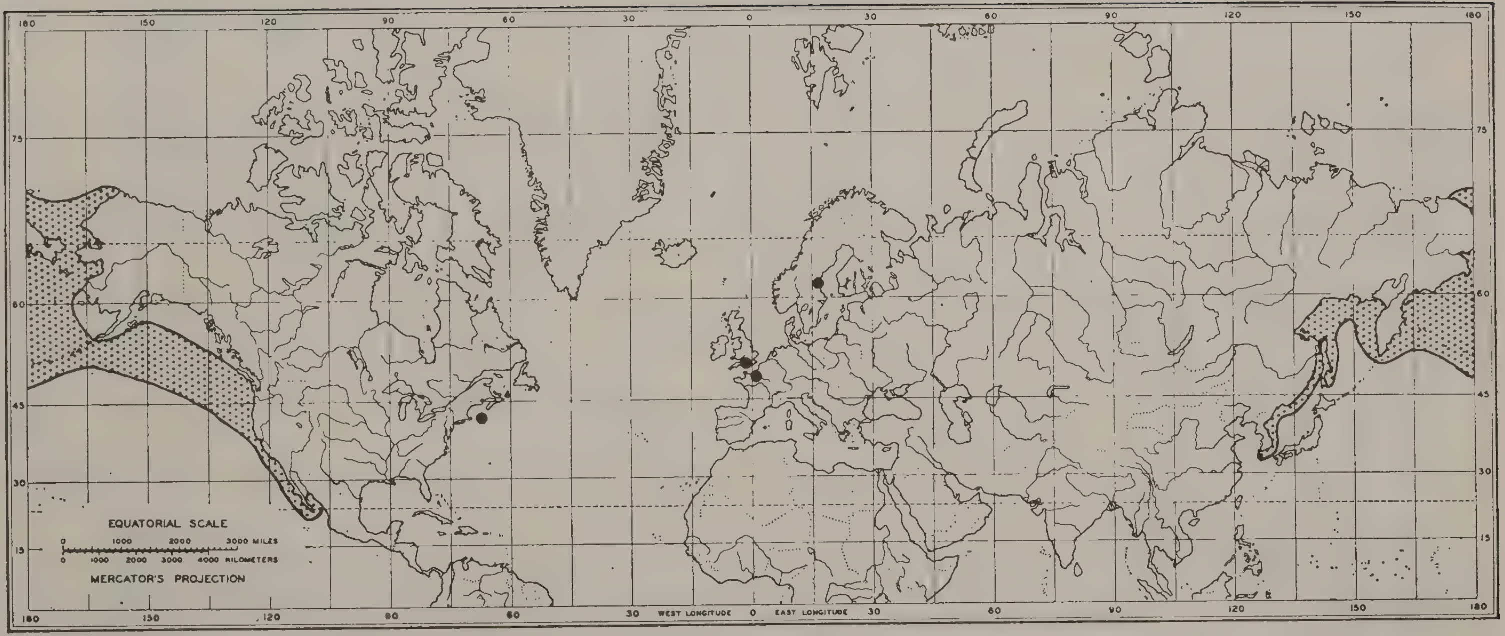

EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE
180
150
120
90
60
30
0
75
45
15

Fig. 46. Distribution of Eschrichtiidae. Note dots in Europe and eastern North America at places of former occurrence.

Recent Distribution. Living in North Pacific Ocean and Chukchi Sea; extinct in North Atlantic.

Recent Genera. (1, 1 Recent species)

Eschrichtius Gray, 1864 (1) [= *Rhachianectes* Cope, 1869]

Geologic Range. Recent in North Atlantic and North Pacific.

Major Fossil Groups. None.

Remarks. This family was formerly called Rhachianectidae Weber, 1904. The living gray whale is closely related to the extinct family *Cetotheriidae.

FAMILY BALAENOPTERIDAE Gray, 1864
Rorquals

Diagnosis. Nasals and nasal processes of premaxillae extending backward beyond level of anterior border of supraorbital processes of frontals; maxillae with nasal processes; nasals reduced; frontals scarcely or not at all exposed on vertex; parietals extending forward laterally beyond level of posterior border of nasals and nasal processes of maxillae and premaxillae; supraoccipital extending forward beyond level of zygomatic process of squamosal; rostrum broad and flat; mandible conspicuously bowed outward; cervical vertebrae separate; numerous parallel grooves covering entire throat and chest region; tongue soft and fleshy; baleen plates short, broad; left and right baleen rows continuous anteriorly.

General Characters. *Balaenoptera* long, slender, streamlined, having snout pointed and dorsal fin falcate. *Megaptera* robust, having long narrow flippers and flukes irregularly scalloped on posterior margins; knobs on snout, lower jaws, chin, and anterior margin of flippers; low dorsal hump, small fin, crenulate dorsal ridge on tail. Length of sexually mature adults from a minimum of 6.7 m. in *Balaenoptera acutorostrata* to a maximum of 31.0 m. in *B. musculus;* a female *B. musculus* 27.1 m. long weighed 136,400 kg. (calculated weight of a 30.0 m. individual would be about 160,000 kg.); females larger than males; races of *Balaenoptera* in the Southern Hemisphere generally larger than those in the Northern Hemisphere; *Balaenoptera* gray above, with varying pattern of white below, depending on species (coloration asymmetrical on head of *B. physalus*); *Megaptera* uniformly black, or with varying amounts of white below.

Habits. During summer, most species of rorquals inhabit high latitudes and the cold currents on the eastern sides of the oceans, where they feed heavily and put on a thick layer of blubber. They feed primarily on dense shoals of "krill," small, red, shrimplike crustaceans of the family Euphausiidae, particularly *Euphausia, Thysanoessa,* and *Meganycti-*

phanes. In the Northern Hemisphere they also take small schooling fishes such as anchovies (*Engraulis*) and sauries (*Cololabis*), and sei whales, *Balaenoptera borealis,* feed to a great extent on calanoid copepods. In autumn, rorquals migrate several thousand kilometers toward equatorial waters; during the winter breeding season, they fast for several months, living off blubber stores. The annual cycles of the Northern and Southern Hemisphere populations are out of phase by 6 months, resulting in genetic isolation. An exceptional species is Bryde's whale, *B. edeni,* which inhabits the equatorial belt within the 20° C. surface water isotherms.

The large rorquals attain sexual maturity at an age of about 10 (6–16) years—see *Remarks* below; the minke whale, *Balaenoptera acutorostrata,* possibly may be sexually mature at an age of only 2 or 3 years.

Female rorquals are seasonally monestrous, but if not impregnated, they rarely may ovulate two or three times during one estrous cycle. A postparturient estrus may occur, but is rare except in the minke whale. A postlactational estrus may occur in the summer in at least some species of *Balaenoptera,* but it rarely results in conception, because the males are usually not fertile at that season. Gestation lasts about 10 months in the minke whale, 10.75 months in the blue whale (*Balaenoptera musculus*), 11.25 months in the fin whale (*B. physalus*), and 12 months in the sei whale (*B. borealis*) and the humpback whale (*Megaptera novaeangliae*). Lactation lasts about 6 months in *Balaenoptera,* close to a year in *Megaptera.* Except in the minke whale, females rarely bear a calf 2 years in succession. Rorquals are most often seen in pods of two to five. When surfacing, most species blow 5 to 10 times, then sound for 5 to 10 minutes; sei whales usually blow regularly about once a minute. "Breaching," "lobtailing," and "finning" are conspicuous behaviorisms of the humpback.

Before intensive commercial exploitation began, there were about 200,000 fin whales, more than 30,000 blue whales, and more than 20,000 humpback whales in the Southern Hemisphere. These three species are the mainstay of the modern whaling industry, and during the last 20 years up to 40,000 have been killed annually the world over by as many as 400 catcher boats operating from about two dozen floating factories and about 50 shore stations. The International Whaling Commission has been ineffective in implementing rational exploitation. As a result, in the Southern Hemisphere the stocks of fin whales have been reduced to less than 20 per cent of their original numbers. Blue and humpback whales are commercially extinct. North Pacific fin whale stocks are now being excessively exploited. (For references, see *Remarks.*)

Habitat. Exclusively oceanic.

Recent Distribution. All oceans. Not mapped.

Recent Genera. (2, 6 Recent species)

Balaenoptera Lacépède, 1804 (5) [incl. *Sibbaldus* Gray, 1864]
Megaptera Gray, 1846 (1)

Geologic Range. Upper Miocene to Pleistocene in North America; early Pliocene to Pleistocene in Europe; Miocene in Asia; Recent in all oceans.

Major Fossil Groups. Seven extinct genera.

Remarks. The modern whaling industry has provided both the stimulus and the opportunity for intensive research on the rorquals, particularly the fin whale and the humpback whale; as a result, their biology is in some respects better known than that of most other large wild mammals, although many aspects are still poorly understood. A selection of recent references, as well as some of the more important older references, is listed below.

General: Chapman *et al.* (1964); Mackintosh (1942, 1965); Mackintosh and Brown (1956); Nemoto (1959); Omura (1950). Blue whale (*Balaenoptera musculus*): Brown (1962); Ichihara (1961); Mackintosh and Wheeler (1929); Nishiwaki (1951); Ruud *et al.* (1950). Fin whale (*B. physalus*): Brown (1962); Jonsgård (1952); Laws (1961); Mackintosh and Wheeler (1929); Nishiwaki (1951); Nishiwaki *et al.* (1958); Ohsumi *et al.* (1958); Purves and Mountford (1959). Sei whale (*B. borealis*): Andrews and Schulte (1916); Matthews (1938*b*); Omura and Nemoto (1955). Bryde's whale (*B. edeni*): Best (1960); Olsen (1913); Omura (1959, 1962). Little piked whale (*B. acutorostrata*): Jonsgård (1951); Omura and Sakiura (1956); Williamson (1961). Humpback whale (*Megaptera novaeangliae*): Chittleborough (1965, and earlier papers); Dawbin (1956); Matthews (1938*a*); Nishiwaki (1959); Omura (1953); Symons and Weston (1958). Important periodicals: *Scientific Reports of the Whales Research Institute* (Tokyo); *Discovery Reports* (National Institute of Oceanography, Wormley, England); *Norsk Hvalfangst-Tidende* (International Association of Whaling Companies, Sandefjord); *Hvalrådets Skrifter* (Statens Institutt for Hvalforskning, Oslo); *International Whaling Statistics* (Bureau of International Whaling Statistics, Sandefjord).

Judgment on the age of sexual maturity in the large rorquals (see *Habits* above) is based on the assumption that one ear plug lamination is formed each year. Until recently, it was believed (on the basis of virtually no evidence) that two laminations were formed each year. Data on ear plugs recently collected from fin whales marked over 25 years ago contradict this hypothesis. These data, and several independent lines of indirect evidence, are consistent with the hypothesis that only one lamination is formed each year (Ohsumi, 1964*a*). Data on ear plugs from whales marked as calves are needed before this question can be conclusively settled.

ORDER ODONTOCETI

Diagnosis. Teeth always present, monophyodont, homodont (except *Inia*), single-rooted, uncusped (except superfamily Squalodontoidea)—although weakly two- or three-lobed in Phocoenidae, and with a well-developed cingulum in *Inia;* number primarily increased over basic eutherian number of 44, but secondarily reduced in many forms, to as few as 0/1 or 1/0; no baleen; skull asymmetrical; maxillae without orbital plates; ascending processes of maxillae large and broad, not interlocking with frontals, spreading outward over the expanded supraorbital processes; nasal bones forming no part of roof of narial passage; single narial opening; narial passages complex, a system of air chambers between external valve and internal plugs; respiratory and alimentary tracts separated by a tubular elongation of epiglottis and arytenoid cartilage which is held in the choanae by the palatopharyngeal sphincter; cartilaginous tracheal rings closed; mandibular symphysis ankylosed; anterior ribs double-headed; sternal ribs present (cartilaginous in Ziphiidae, Physeteridae, Platanistinae, and Iniinae, but ossified in all other groups); sternum consisting of three or more sternebrae, articulating with three or more pairs of ribs.

Recent Distribution. All oceans and contiguous seas, and certain rivers and lakes of Africa, Asia, North America, and South America.

Geologic Range. Late Eocene to Recent.

Families. (12, 33 Recent genera, *ca.* 74 Recent species)

- *SUPERFAMILY SQUALODONTOIDEA
  - *Agorophiidae
  - *Squalodontidae
- SUPERFAMILY ZIPHIOIDEA
  - Ziphiidae
- SUPERFAMILY MONODONTOIDEA
  - Monodontidae
- SUPERFAMILY PHYSETEROIDEA
  - Physeteridae
- SUPERFAMILY PLATANISTOIDEA
  - Platanistidae
- SUPERFAMILY DELPHINOIDEA
  - *Eurhinodelphidae
  - *Hemisyntrachelidae
  - *Acrodelphidae
  - Stenidae
  - Phocoenidae
  - Delphinidae

Remarks. The family classification here employed is basically that of Slijper (1936), later modified by Simpson (1945*a*), and further extended, in respect to Recent forms, by Fraser and Purves (1960). According to Fraser (*in litt.*), the taxonomy of the Delphinoidea will require much more study before a definite arrangement can be proposed.

In two recent papers, Nishiwaki (1963, 1964) divided the living Delphinoidea into five families—Delphinidae, Orcellidae, Phocaenidae, Globicephalidae, and Grampidae. These are diagnosed primarily on the basis of the number of teeth, number of fused cervical vertebrae, and shape of the snout. He also separated *Kogia* as a monotypic family Kogiidae. He recognized no subfamilies or superfamilies; all taxa between genus and order were ranked as families.

Some of the important earlier works on odontocete taxonomy are those of Winge (1921), Miller (1923), and Kellogg (1928).

FAMILY ZIPHIIDAE Gray, 1865
Beaked whales

Diagnosis. Rostrum narrow and deep, with open mesirostral groove (in older animals closed by a dorsal expansion and ossification of the vomer); occipital crest prominent; palatines forming part of anterior wall of narial passage; mesial lamina of pterygoid much enlarged; lateral lamina small, ventrodorsally compressed, and horizontally disposed; pterygoid hamulus enlarged and distended posteriorly and anteriorly; air-sinus system simple, without preorbital and postorbital lobes; two to seven cervical vertebrae fused.

General Characters. Medium to moderately large, proportions slender; dorsal fin small, placed posteriorly; one pair of grooves on throat; posterior margin of flukes not deeply notched at midline; snout long and narrow, sharply demarked from high bulging forehead in *Hyperoodon* and *Berardius,* forming a continuous smooth profile with head in other genera; length of adults from about 4.0 m. in *Mesoplodon* to a maximum of 12.4 m. in *Berardius bairdii;* weight of a female *B. bairdii* (11.1 m.) was 11,380 kg.; males markedly larger than females in *Hyperoodon,* but females slightly larger in *Berardius* and *Ziphius;* color usually uniform brownish to grayish, sometimes lighter ventrally, or with white ventral splotches; functional teeth about 19/27 in *Tasmacetus,* reduced to 0/2 in *Berardius,* and normally 0/1 in the other genera; teeth usually buried in gums in females; additional minute vestigial teeth, lacking alveoli, often present in gums.

Stomach of four to 14 chambers, but no esophageal chamber (corresponding to first chamber of other odontocetes). The genus *Mesoplodon* exhibits, in the males, several remarkable specializations of the single pair of teeth; in some species they are small and anterior to the symphysis; in others they are large, laterally compressed, and posterior to the symphysis; in *M. layardi* they curve over the upper jaw and prevent the mouth from being widely opened; in *M. densirostris* they are located at the summit of vertical expansions of the rami, and protrude above the forehead somewhat like a pair of horns. In *Berardius* the lower jaw protrudes beyond the upper, so that the anterior pair of teeth are completely outside the mouth.

Habits. Little is known of the biology of the beaked whales. Like sperm whales, they are deep divers; when harpooned, *Berardius* is alleged to descend to 2400 m. The giant bottle-nosed whale, *Berardius bairdii*, normally remains down 15 to 20 minutes, then surfaces for about five minutes, blowing about 20 times. The North Atlantic bottle-nosed whale (*Hyperoodon ampullatus*), which normally remains submerged for 30 to 45 minutes, has been reported to stay down as long as two hours. All beaked whales feed chiefly on small- to medium-sized squids, but also eat deep sea fishes. Annual migrations are performed by *H. ampullatus* and probably by other species. The giant bottle-nosed whale of the North Pacific mates in February and gives birth in December; gestation is believed to last about 10 months; the age at sexual maturity is probably three or more years. Giant bottle-nosed whales are highly sociable; their tightly packed schools consist of a dozen or more individuals which surface and dive in unison. North Atlantic bottle-nosed whales also are sociable, but goose-beaked whales (*Ziphius cavirostris*), and probably also the whales of the genus *Mesoplodon*, are usually solitary. The apparent rarity of specimens of the latter is probably owing to their small size, failure to play alongside ships, and lack of commercial value. The bottle-nosed whales (*Hyperoodon* and *Berardius*), and to a lesser extent the goose-beaked whale, are taken commercially off Japan and Norway (Omura *et al.*, 1955).

Habitat. Exclusively oceanic.

Recent Distribution. All oceans. Not mapped.

Recent Genera. (5, 18 Recent species)

Berardius Duvernoy, 1851 (2)
Hyperoodon Lacépède, 1804 (2)
Mesoplodon Gervais, 1850 (12) [= *Nodus* Wagler, 1830, *nomen oblitum*]
Tasmacetus Oliver, 1937 (1)
Ziphius G. Cuvier, 1823 (1)

Geologic Range. Early Miocene to Pliocene in South America; early Miocene to middle Pliocene in Europe; late Miocene to Pliocene in North America; Recent in all oceans.

Major Fossil Groups. Fourteen extinct genera.

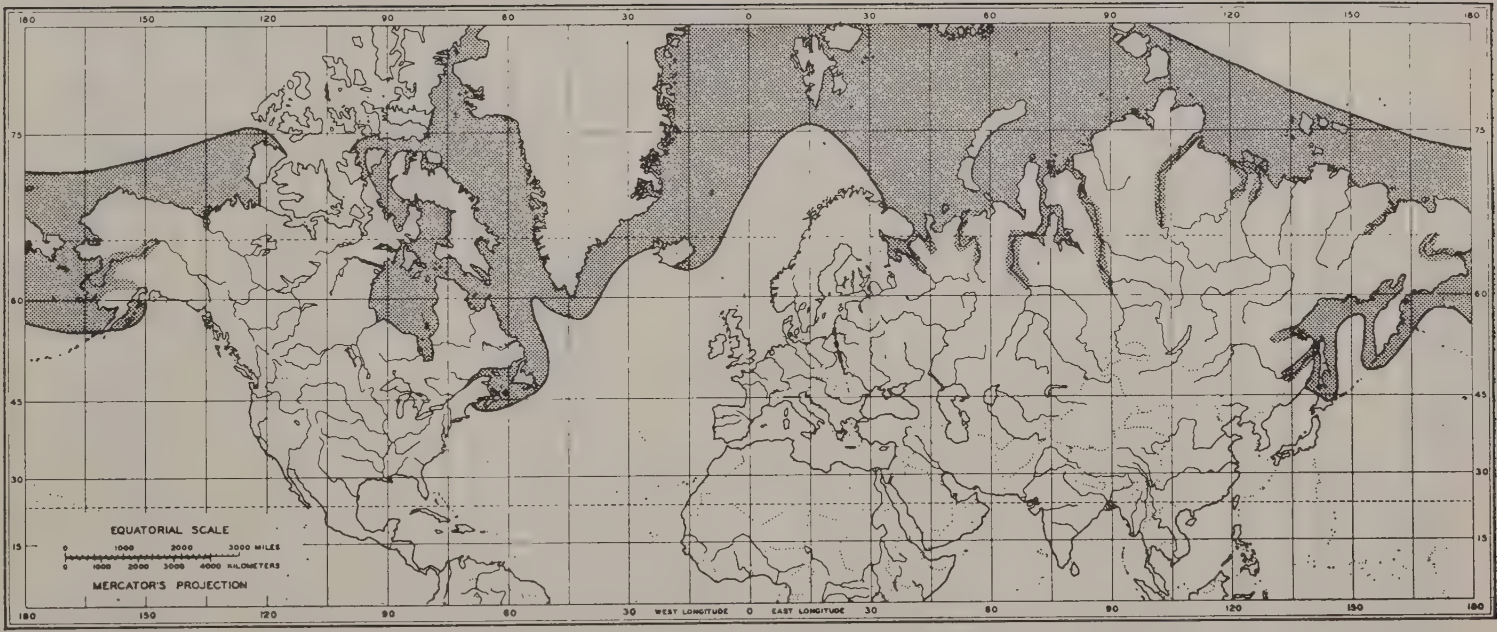
Remarks. True (1910) reviewed the family.

FAMILY MONODONTIDAE Gray, 1821
Narwhal and beluga

Diagnosis. Cranial features generalized, similar to the Delphinoidea, and without the specialized features of the Physeteroidea; air-sinus system similar to that of the Physeteroidea, much simplified; pterygoid sinus without preorbital and postorbital processes; all cervical vertebrae free.

General Characters. Medium-sized; male belugas (*Delphinapterus leucas*) attain a maximum length of 5.8 m. and a maximum weight of about 2000 kg., male narwhals (*Monodon monoceros*) reach a length (exclusive of the tusk) of 6.1 m., females of both species smaller; forehead high and globose; short, broad snout in beluga, snout virtually absent in narwhal; a slight neck apparent; no dorsal fin, although a long, low dorsal ridge present on the back; flippers short, broad, and rounded; calves at birth dark brown, later changing to gray, and finally to pure white in the adult beluga and mottled gray in the adult narwhal; teeth number about 9/9 in *Delphinapterus,* 1/0 in *Monodon;* in the male narwhal, the left (rarely the right) tooth is normally developed into a straight, forwardly directed, helically grooved tusk up to 2.7 m. long (females rarely have tusks); paired tusks are sometimes found, usually on females; tusks always have a sinistral spiral (even if paired, both spiral in the same direction).

Habits. Belugas and narwhals are characteristic animals of the arctic pack ice. They are gregarious and during the winter congregate in areas kept open by tides, currents, or wind, or retreat only as far as the edges of the ice; when necessary they break their way up through thin ice. In spring they push northward as soon as leads begin to open in the ice. During summer belugas may ascend several hundred kilometers up the larger arctic rivers. Belugas feed on a wide variety of benthic and midwater organisms; young animals feed largely on small bottom-living crustaceans, while older animals change to a more varied diet consisting largely of fish, including capelin (*Mallotus villosus*), Arctic char (*Salvelinus alpinus*), Atlantic cod (*Gadus morhua*), Greenland cod (*Gadus ogac*), Arctic cod (*Boreogadus saida*), Atlantic tomcod (*Microgadus tomcod*), American sand lance (*Ammodytes americanus*), and Arctic sculpin (*Myoxocephalus scorpioides*), but also eat squid (*Illex illecebrosus*), and annellid worms (*Nereis virens*). Narwhals are believed to be more pelagic feeders; in some areas they feed primarily on the abundant Arctic cod (*Boreogadus saida*); some authorities believe they feed


180
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EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE

Fig. 47. Distribution of Monodontidae.

largely on cephalopods (*Rossia; Gonatus,* etc.); other reported food items are "halibut," "flounder," "skate," "salmon," and "herring."

Absolute age at sexual maturity is not known, but in the beluga it corresponds to the accumulation of about 12 dentinal laminations in the female, 12 to 18 in the male (Sergeant, 1959). In the beluga, at least, the ovaries are functionally asymmetrical, about 80 per cent of ovulations occurring in the left ovary. Pairing takes place in the spring, earlier in the low Arctic, later in the high Arctic. The gestation period is 14 months. Lactation lasts about 6 months. Females bear a calf no more than once every 2 years. Maximum longevity is indicated by animals with about 50 dentinal laminations. Belugas are an important source of food for the Eskimos of Canada, Alaska, and Greenland. Commercial hunting for belugas is conducted at Spitzbergen, the Soviet Arctic and Far East, Kotzebue in Alaska, Pangnirtung on Baffin Island, at Churchill on Hudson Bay, and until recently in the St. Lawrence River (Degerbøl and Freuchen, 1935; Doan and Douglas, 1953; Kleinenberg *et al.*, 1964; Vladykov, 1944 and 1946).

Habitat. Oceanic and neritic, primarily in the arctic pack ice. *Delphinapterus* may be fluviatile and estuarine during the summer.

Recent Distribution. Arctic Ocean, Bering Sea, and Okhotsk Sea; also most of the larger rivers of Siberia, the Yukon and Kuskokwim Rivers in Alaska, and the St. Lawrence River in eastern Canada.

Recent Genera. (2, 2 Recent species)

Delphinapterus Lacépède, 1804 (1)
Monodon Linnaeus, 1758 (1)

Geologic Range. Pleistocene to Recent in Arctic.

Major Fossil Groups. No extinct genera have been discovered.

Remarks. The narwhal and beluga are sometimes placed in separate subfamilies, Monodontinae and Delphinapterinae, respectively (Miller and Kellogg, 1955). They have been placed under the family Delphinidae, either together as one subfamily (True, 1889), or separately as two subfamilies (Miller, 1923; Kellogg, 1928). Fraser and Purves (1960) have demonstrated that they deserve to be allocated to a separate superfamily, the Monodontoidea.

FAMILY PHYSETERIDAE Gray, 1821

sperm whales

Diagnosis. Rostrum broad and flat; facial depression great, accommodating a highly developed spermaceti organ (the "case") bounded posteriorly by a high occipital crest; palatines not forming part of anterior wall of narial passage; air-sinus system simple, no preorbital and postorbital processes.

General Characters. *Physeter* with enormous head, about 35 per cent total length in adult males, containing huge barrel-shaped spermaceti organ; *Kogia* with smaller head, exceptionally short and broad rostrum; blowhole sigmoid, on left side of anterior end of snout; left nasal passage functioning in respiration, the right one modified as a sound production organ; upper jaw extending conspicuously beyond lower; dorsal fin falcate in *Kogia,* obtuse or rounded in *Physeter;* crenulate dorsal ridge and thick ventral keel on tail in *Physeter;* throat with numerous short grooves; body of *Physeter* with broad, shallow, irregular, longitudinal corrugations.

Length of sexually mature adults 2.1 to 3.4 m. in *Kogia,* 8.8 to 12.3 m. in female *Physeter,* and 9.4 to about 18.0 m. in male *Physeter* (a male *Physeter* 18.2 m. long weighed 53,364 kg.); males much larger than females in *Physeter,* only slightly so in *Kogia;* color uniform slate gray, sometimes with white blotching underneath; about 0/25 functional teeth in *Physeter;* gingival eruption does not occur until after the attainment of sexual maturity; 0/8 to 0/16 teeth in *Kogia;* vestigial teeth present in upper jaw in *Physeter* and in *Kogia simus,* absent in *K. breviceps* (the extinct subfamily *Hoplocetinae possessed functional maxillary teeth); mandible narrow with long symphysis in *Physeter,* broad with short symphysis in *Kogia;* atlas free, remaining cervical vertebrae fused in *Physeter;* all cervicals fused in *Kogia.*

Habits. Sperm whales are deep divers; they regularly descend to depths of over 900 m., and have been recorded as deep as 1130 m. (Heezen, 1957). They may remain submerged for from 20 minutes to over an hour, then surface and blow 20 to 70 times. The giant sperm whale, *Physeter catodon,* feeds mostly on medium-sized to large squids, including the giant squids (*Architeuthis* and *Moroteuthis*), but also takes many demersal and bathypelagic sharks, skates, and fishes; pygmy sperm whales, *Kogia breviceps* and *K. simus,* also feed mostly on cephalopods (including *Sepioteuthis australis* and *Sepia officinalis*), but take also shrimps (*Pasiphaea pacifica, Pandalus ?borealis, Pandalopsis ?dispar, Penaeus* sp., and *Hymenodora* sp.), green crabs (*Carcinides maenas*), and sandfish (*Trichodon trichodon*). Many male giant sperm whales migrate to high latitudes (as far as the edge of the pack ice) during summer months; females usually remain in tropical and temperate waters, and are rare in latitudes higher than 50°.

Sexual maturity is attained at about 8 years in *Physeter.* This estimate is based on the assumption that one dentinal lamination is formed each year. Recent investigations indicate that this is probably the case (Ohsumi *et al.*, 1963). Data on teeth from sperm whales marked as calves are needed before this can be conclusively proven. Sexual maturity is attained allegedly at only 2 years in *Kogia*. Females of *Physeter* bear one calf every 4 or 5 years. In temperate waters, at least, mating occurs in spring, parturition in summer of the following year, after 15.5 months of gestation. Lactation lasts about 2 years. Pygmy sperm whales may mate in late summer and parturition may occur in spring; a gestation period of only 9 months has been suggested, but this is questionable. Calves are weaned at an age of about 1 year. Females simultaneously pregnant and lactating have been found, indicating that they may bear a calf two years in succession. Maximum longevity of the giant sperm whale may be more than 60 years. They are gregarious, and congregations may contain as many as 100 or rarely even 1000 individuals; also, they are polygynous, and exhibit a well-marked social organization. Females with calves and subadults of both sexes usually travel together in tight groups called maternity, or nursery, schools. One or more large adult bulls ("schoolmasters") may join these groups, forming so-called harem schools. The younger adult males often travel in loose bachelor schools. Many adult males are solitary. The pygmy sperm whale seems to be solitary or to occur in small schools.

Giant sperm whales are an important species in the modern whaling industry, more than 25,000, the majority males, being killed annually in recent years; particularly large numbers are caught off the coasts of Peru and Chile and in the North Pacific. A few pygmy sperm whales are included in the commercial catch at Japanese shore stations (Allen, 1941; Clarke, 1956; Nishiwaki *et al.*, 1958).

Habitat. Exclusively oceanic.

Recent Distribution. All oceans. Not mapped.

Recent Genera. (2, 3 Recent species)

- Subfamily Physeterinae
  - *Physeter* Linnaeus, 1758 (1)
- Subfamily Kogiinae
  - *Kogia* Gray, 1846 (2)

Geologic Range. Subfamily *Hoplocetinae: early Miocene in South America; early to late Miocene in Europe; middle Miocene in North America; early Pliocene in Australia. Subfamily Physeterinae: middle to late Miocene and Pleistocene in North America; early to late Miocene and middle Pliocene in Europe; early Pliocene in Australia; Recent in all oceans. Subfamily Kogiinae: early Pliocene in North America; late Pliocene in Japan; Recent in all oceans.

Major Fossil Groups. One extinct subfamily, *Hoplocetinae, with six genera; 13 extinct genera of Physeterinae, and one of Kogiinae.

Remarks. The Kogiinae are sometimes ranked as a family (Miller, 1923; Kellogg, 1928).

FAMILY PLATANISTIDAE Gray, 1863
Long-snouted river dolphins

Diagnosis. Facial depression narrow, maxilla and frontal not roofing over the large temporal fossa; external border of maxilla with longitudinal crest; palatines not united at midline, widely separated by vomer; zygomatic process of squamosal well developed, strongly projecting and arched; jaws exceedingly long and narrow, the tooth-rows close together and parallel; mandibular symphysis approximately one-half the length of the rami; air-sinus system complex, with preorbital and postorbital processes; all cervical vertebrae separate.

General Characters. Small; long slender beak sharply demarked from bulging forehead; neck distinct, dorsal fin low, obtuse; flippers broad; length of adults from 1.5 m. in *Pontoporia* to 2.9 m. in *Platanista;* weight of a female *Pontoporia* (1.72 m.) was 40.0 kg., that of a male *Inia* (2.28 m.) was 122.8 kg.; females slightly larger than males; color blackish in *Platanista,* brownish in *Pontoporia,* and pale tending toward whitish in *Inia* and *Lipotes;* teeth from about 55/55 in *Pontoporia* to about 26/26 in *Inia;* roots laterally compressed in *Platanista;* well-developed cingulum on lingual side of posterior teeth in *Inia; Platanista* has no eye lenses and is totally blind; eyes of *Lipotes* greatly reduced and almost nonfunctional; eyes of *Inia* small, but apparently fully functional.

Habits. The blind susu (*Platanista gangetica*) of the Ganges River feeds on fresh-water shrimps and mud-frequenting fishes which it catches by probing about in the bottom of the river; the pei c'hi, or white-flag dolphin (*Lipotes vexillifer*), of Tungt'ing Lake, China, eats eel-like catfish which it catches by working up the mud in shallow water; the bouto (Portuguese) or bufeo (Spanish), *Inia geoffrensis,* of the upper Amazon apparently feeds exclusively on fishes, which it captures by pursuit or by stalking. The La Plata dolphin, or franciscana (*Pontoporia blainvillei*), feeds on herring (Clupeidae), prawns (*Penaeus*), and squid (*Loligo*) off the Brazilian coast. Migratory movements of river dolphins are apparently of limited extent; the pei c'hi is said to migrate up the small clear mountain rivers which empty into Tungt'ing Lake during the late spring rainy season; the franciscana deserts the La Plata Estuary and moves to the open coast during winter. During periods of high water, the bouto may leave the main river channels and travel for some distance into the flooded forests. Virtually nothing is known about reproduction in river dolphins; the susu is said to mate from July to September, and to give birth from April to July after 8 to 9 months of gestation (such a short gestation period is highly questionable); the pei c'hi is believed to breed during late spring. The platanistids are not very gregarious; they usually go about in schools of less than a dozen (Anderson, 1878; de Carvalho, 1961; Hoy, 1923; Layne, 1958; Layne and Caldwell, 1964).

Habitat. Subfamilies Platanistinae and Iniinae are fluviatile; the subfamily Pontoporiinae is estuarine and neritic.

Recent Distribution. Indus, Ganges, and Brahmaputra river systems of India (subfamily Platanistinae); Amazon and Orinoco river systems of South America and Tungt'ing Lake, China (subfamily Iniinae); La Plata Estuary and coast of South America from central Brazil to central Argentina (subfamily Pontoporiinae).

Recent Genera. (4, 4 Recent species)

SUBFAMILY PLATANISTINAE
  Platanista Wagler, 1830 (1) [= *Susu* Lesson, 1828, *nomen oblitum*]
SUBFAMILY PONTOPORIINAE
  Pontoporia Gray, 1846 (1) [= *Stenodelphis* D'Orbigny and Gervais, 1847]
SUBFAMILY INIINAE
  Inia D'Orbigny, 1834 (1)
  Lipotes Miller, 1918 (1)

Geologic Range. Subfamily Platanistinae: middle Miocene in North America; late Miocene in Europe; Recent in Southeastern Asia. Subfamily Iniinae: early Miocene to Recent in South America; early Pliocene in North America; Recent in Southeastern Asia. Subfamily Pontoporiinae: middle Pliocene and Pleistocene in North America; Pliocene and Recent in South America.

Major Fossil Groups. Two extinct genera of Platanistinae, six of Iniinae, and three of Pontoporiinae.

Remarks. Miller (1923) and Kellogg (1928) ranked the Platanistinae and Iniinae each as a family, and transferred Pontoporiinae ("Stenodelphininae") to the family Delphinidae; they attributed to convergence the similarities between these three groups. Slijper (1936) believed them to be related, and placed them together in the family Platanistidae, without recognizing subfamilies. Simpson (1945*a*) and Fraser and Purves (1960) regarded them as three distinct subfamilies of a single family.

FAMILY STENIDAE Fraser and Purves, 1960

Diagnosis. Distinguished from the Delphinidae, which it otherwise resembles, by the combination of two features of the air-sinus system—(1) the attenuated extension of the postorbital lobe of the pterygoid sinus under the postorbital process of the frontal, and (2) the lateral expansion

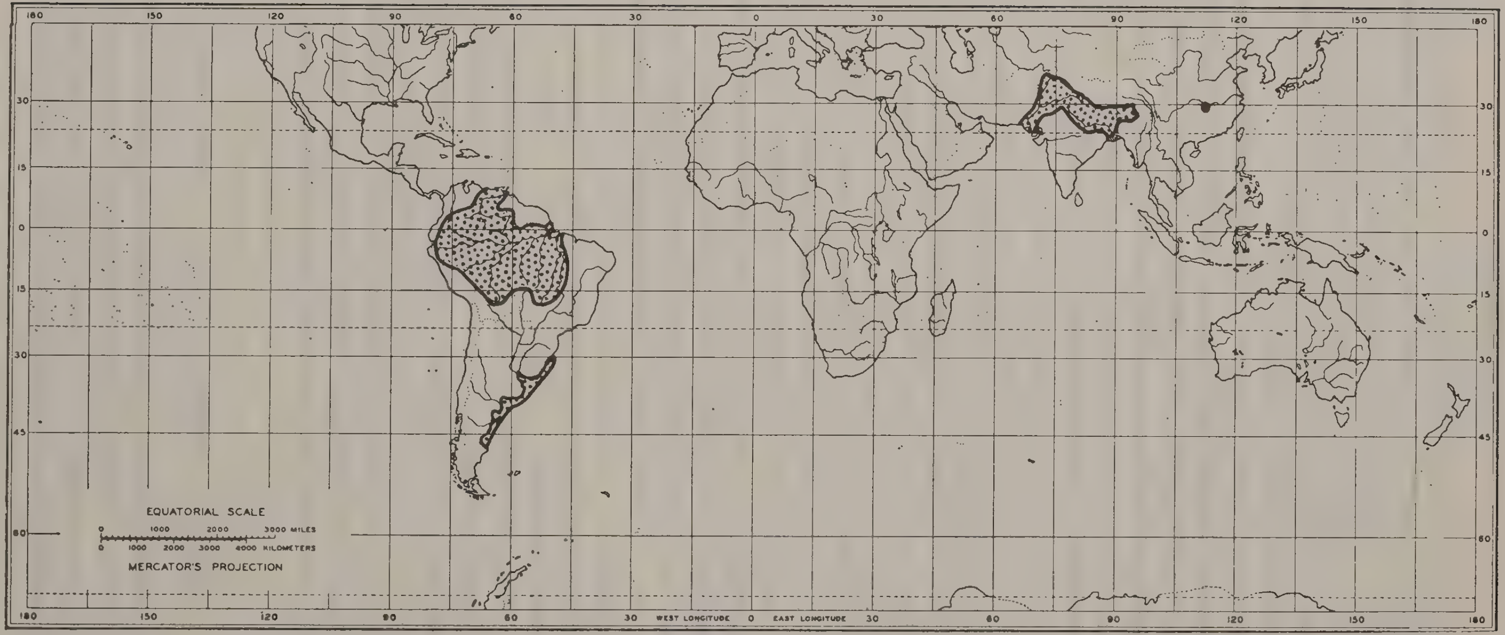
EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE

Fig. 48. Distribution of Platanistidae. Do not overlook the dot for Tungt'ing Lake in China.

of the preorbital and postorbital lobes, which coalesce above the optic infundibulum; in *Steno* and *Sousa,* the mandibular symphysis is greater than 30 per cent of the length of the rami; atlas and axis fused.

General Characters. Size moderately small; an adult male *Steno bredanensis,* 2.23 m. long, weighed 102 kg., an adult male *Sousa teuszi,* 2.48 m. long, weighed 166 kg., whereas an adult male *Sotalia guianensis,* 1.61 m. long, weighed 48 kg.; snout long, but not sharply demarked from the forehead, the dorsal profile forming a continuous smooth curve (in *Sousa teuszi* and the species of *Sotalia,* there is a moderate demarcation of snout from forehead); snout of *Steno* laterally compressed; falcate dorsal fin present in *Steno* and *Sotalia.* Dorsal fin only slightly concave posteriorly in *Sousa,* and located at the summit of a long, narrow dorsal "hump"; flippers broad at base; *Steno* is dark gray on the back, light gray on the sides, and white on the underparts (sometimes including the snout), the colors sharply demarked from each other; the freshwater species (*Sousa chinensis* and *Sotalia fluviatilis*) of the other two genera are nearly pure white when adult, whereas the marine species are speckled (*Sousa lentiginosa*), or gray; average number of teeth about 24/24 in *Steno,* 32/32 in *Sousa* and *Sotalia;* crowns of teeth are rugose in *Steno.*

Habits. Very little is known of the biology of these dolphins. The rough-toothed dolphin (*Steno bredanensis*) appears to be rare. The stranding of one school of over 100 individuals has been reported. The stomachs of specimens from Senegal and the Ivory Coast contained remains of squid and unidentified fish; several from the Gulf of Mexico contained the pelagic blanket octopus, *Tremoctopus violaceus.* The testes of males taken in July, September, and October off West Africa were in active spermatogenesis; four females from Senegal and the Ivory Coast were carrying fetuses 0.60 to 0.87 m. long in May. The species of *Sousa* and *Sotalia* inhabit coastal waters and estuaries, and often ascend the lower reaches of large rivers; the tucuxi (*Sotalia fluviatilis*) of the Amazon basin is confined to fresh water, and even penetrates deep into inundated forests during periods of high water. The tucuxi is usually observed in groups of two or three. Herring-like fish and small catfish have been found in the stomach of the Guiana river dolphin (*Sotalia guianensis*); the tucuxi has been observed chasing fish. Teusz's dolphin (*Sousa teuszi*) of West Africa usually feeds on fishes, including mullet (*Mugil*), herring (*Ethmalosa*), and grunters (*Pristipoma*). The oft-repeated statement that this species is herbivorous resulted from confusion with the manatee (*Trichechus senegalensis*) (Cadenat and Paraiso, 1957); it is incredible that so many writers have uncritically accepted and repeated such an improbable statement! Nothing seems to be known about reproduction in *Sousa* and *Sotalia.* (Cadenat, 1959; Layne, 1958.

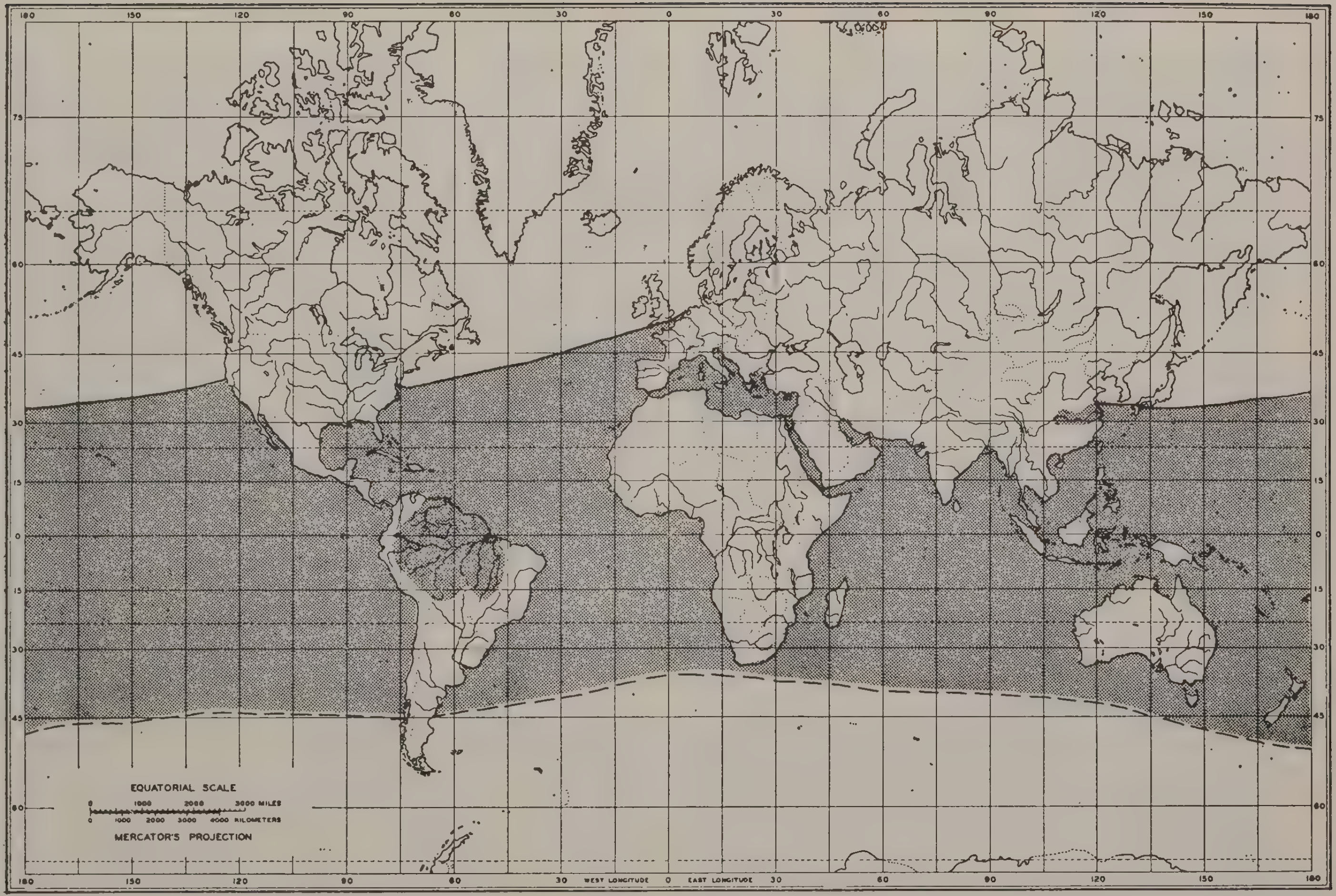
EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE
180 150 120 90 60 30 0 30 60 90 120 150 180
75 60 45 30 15 0 15 30 45 60

Fig. 49. Distribution of Stenidae. Southern limits are poorly known.

Habitat. *Steno* is oceanic; *Sousa* and *Sotalia* are fluviatile, estuarine, or neritic.

Recent Distribution. Tropical and warm temperate waters of all oceans (*Steno*); coastal areas of southern Asia and East Africa from the Yangtze River, China, to Zanzibar, coast of West Africa from Senegal to Cameroon, doubtfully coasts of South Africa (*Sousa*); Amazon and Orinoco river basins and coast of South America from southern Brazil to Venezuela, possibly also Florida (*Sotalia*).

Recent Genera. (3, 8 Recent species)

Sotalia Gray, 1866 (2)
Sousa Gray, 1866 (5)
Steno Gray, 1846 (1)

Geologic Range. *Steno* is known from the early and middle Pliocene in Europe; **Kentriodon* from the middle Miocene in Maryland and **Hesperocetus* from the early Pliocene in California may belong to this family (see below).

Major Fossil Groups. **Kentriodon* and **Hesperocetus* may have been antecedents of the Recent *Sotalia* (R. Kellogg, *in litt.*).

Remarks. This family was recently established by Fraser and Purves (1960) for the genera *Steno* and *Sousa*. When more detailed studies are made, it may be found necessary to place each of these genera in a separate family (F. C. Fraser, *in litt.*). *Sotalia* is only tentatively referred to this family, because of certain similarities to *Sousa* (R. Kellogg, *in litt.*).

FAMILY PHOCOENIDAE Bravard, 1885
Porpoises

Diagnosis. Similar to the Delphinidae in cranial features, but distinguished by prominent bosses on the premaxillae in front of the nares, and by the spadelike teeth with laterally compressed, weakly two-lobed or three-lobed crowns; air-sinus system characterized by the attenuated extension of the preorbital and postorbital lobes of the pterygoid sinus (*Phocoenoides* has not been examined for this feature); three to seven cervical vertebrae ankylosed.

General Characters. Size small; males of *Phocoena phocoena* attain a maximum length of 1.8 m. and a weight of 90 kg., *Neophocaena,* 1.6 m., and *Phocoenoides,* 2.1 m. and 118 kg.; jaws relatively short, no distinct beak; teeth 15/15 to 30/30; dorsal fin low and obtuse in *Phocoena* and *Phocoenoides,* absent in *Neophocaena* (its place taken by low dorsal ridge); color solid blackish, or blackish above and white below in *Phocoena* and *Neophocaena, Phocoenoides* black with conspicuous white "sidewalls" and belly, and white submarginal patches on trailing edges of dorsal fin and flukes.

Phocoenoides has 95 to 100 vertebrae (as opposed to 60 to 70 in *Phocoena* and *Neophocaena*) and up to 18 pairs of ribs, is very deep-bodied, and has a deep caudal peduncle which is produced dorsally and ventrally into a high, narrow keel; the dorsal keel forms a distinct break, or hump, in the dorsal profile immediately anterior to the flukes.

Habits. The porpoises of the genera *Phocoena* and *Neophocaena* inhabit bays, estuaries, and tidal channels, and the green waters close to shore. They are normally slow swimmers, and almost never accompany vessels. They usually travel in small groups of fewer than six, and more than 20 are rarely seen together. The white-flanked porpoises (*Phocoenoides dalli* and *P. truei*) inhabit the clear blue waters over the continental slope in the North Pacific. They are among the swiftest of cetaceans and regularly race ahead of vessels; they almost never leap clear of the water and are usually seen in schools of 4 to 15, but occasionally 100 or more congregate together on favorable feeding grounds. The black finless porpoise (*Neophocaena phocaenoides*) feeds largely on prawns (*Palaemon* and *Penaeus*), but also takes cuttlefishes (*Sepia*), squid (*Loligo*), and unidentified small fishes. Harbor porpoises (*Phocoena phocoena*) feed on a wide variety of small, nonspiny, schooling fishes, principally herring (*Clupea harengus, C. sprattus,* and *Sardinops sagax*) and whiting (*Gadus merlangus*). *Phocoenoides truei* taken in the waters off Japan had been feeding primarily on demersal lantern fishes (family Myctophidae), but also contained squid and a sudid fish (*Paralepis*); *Phocoenoides dalli,* both off Japan and in the eastern North Pacific, feeds almost exclusively on squid, but also takes a few fish (hake, *Merluccius productus* and *Laemonema morosum,* and herring, *Clupea harengus*).

In the harbor porpoise, the female at least, attains sexual maturity at an age of only 14 months and normally breeds every year thereafter. The right ovary of phocoenids is nonfunctional. In the Baltic Sea, harbor porpoises pair in July and August and the young are born in May and June. The gestation period is nearly 11 months. The calves first begin to take solid food at an age of about 5 months, and are fully weaned at 8 months. Large numbers of porpoises are taken commercially in Japan (Allen, 1923; Møhl-Hansen, 1954; Rae, 1965; Scheffer, 1949; Wilke *et al.*, 1953).

Habitat. *Neophocaena* is fluviatile, estuarine, and neritic; *Phocoena* is estuarine and neritic; *Phocoenoides* is oceanic.

Recent Distribution. All oceans and contiguous seas of the Northern Hemisphere, including the Black Sea; coastal waters of temperate South America, the Falkland Islands, and South Georgia; certain rivers of southeastern Asia; questionably reported from South Africa.

Recent Genera. (3, 7 Recent species)

Neophocaena Palmer, 1899 (1) [= *Neomeris* Gray, 1846, not Costa, 1844; *Meomeris* Gray, 1847, misspelling]
Phocoena G. Cuvier, 1817 (4)
Phocoenoides Andrews, 1911 (2)

Geologic Range. Late Miocene in Europe; Pleistocene in Asia and New Zealand; Recent in most oceans.

Major Fossil Groups. Three extinct genera.

Remarks. Some authors have regarded the porpoises as only a subfamily of the Delphinidae, or have merged them with the subfamily Delphininae. Dall's and True's porpoises, genus *Phocoenoides*, are placed by some authors in the genus *Phocoena*. However, they differ widely from the latter genus in osteology, body form, color pattern, habitat, and behavior; more so, in fact, than most genera of the Delphininae differ among themselves. Fraser (*in litt.*) agrees that *Phocoenoides* should not be merged with *Phocoena*. *Neophocaena* is much more closely related to *Phocoena* than is *Phocoenoides*.

FAMILY DELPHINIDAE Gray, 1821
Ocean dolphins

Diagnosis. Facial depression broadly expanded posteriorly, the maxilla and frontal roofing over the small temporal fossa; maxilla not crested; palatines united at midline of palate, not separated by vomer; zygomatic process of squamosal much reduced, not projecting; jaws not exceedingly long and narrow, tooth-rows well separated and diverging posteriorly; mandibular symphysis less than 20 per cent of the length of the rami; air-sinus system complex and variable; preorbital and postorbital processes present, but not as in Stenidae or Phocoenidae; two to six cervical vertebrae ankylosed.

General Characters. Small- to medium-sized; prominent beak sharply demarked from the forehead in the Delphininae (except *Grampus*) and Lissodelphinae; no distinct beak but often a bulging, globose forehead, resulting from a well-developed "melon" (homologous to the spermaceti organ of the Physeteridae) in the Orcininae, Cephalorhynchinae, and *Grampus;* dorsal fin present except in *Lissodelphis;* adults from 1.5 m. long in smaller dolphins to 9.4 m. in *Orcinus orca* (a male *Orcinus orca* 7.6 m. long weighed 6964 kg.); males usually larger than females (in some, marked sexual dimorphism in shape of dorsal fin and flippers, e.g., thickened, hooked dorsal fins, and long, tapering flippers in adult males of *Globicephala,* and unusually high, straight, erect dorsal fins and tremendous paddle-shaped flippers in adult males of *Orcinus*); coloration variable, some forms nearly uniform gray or black, often lighter underneath, some elaborately patterned with stripes, bands, or spots of gray,

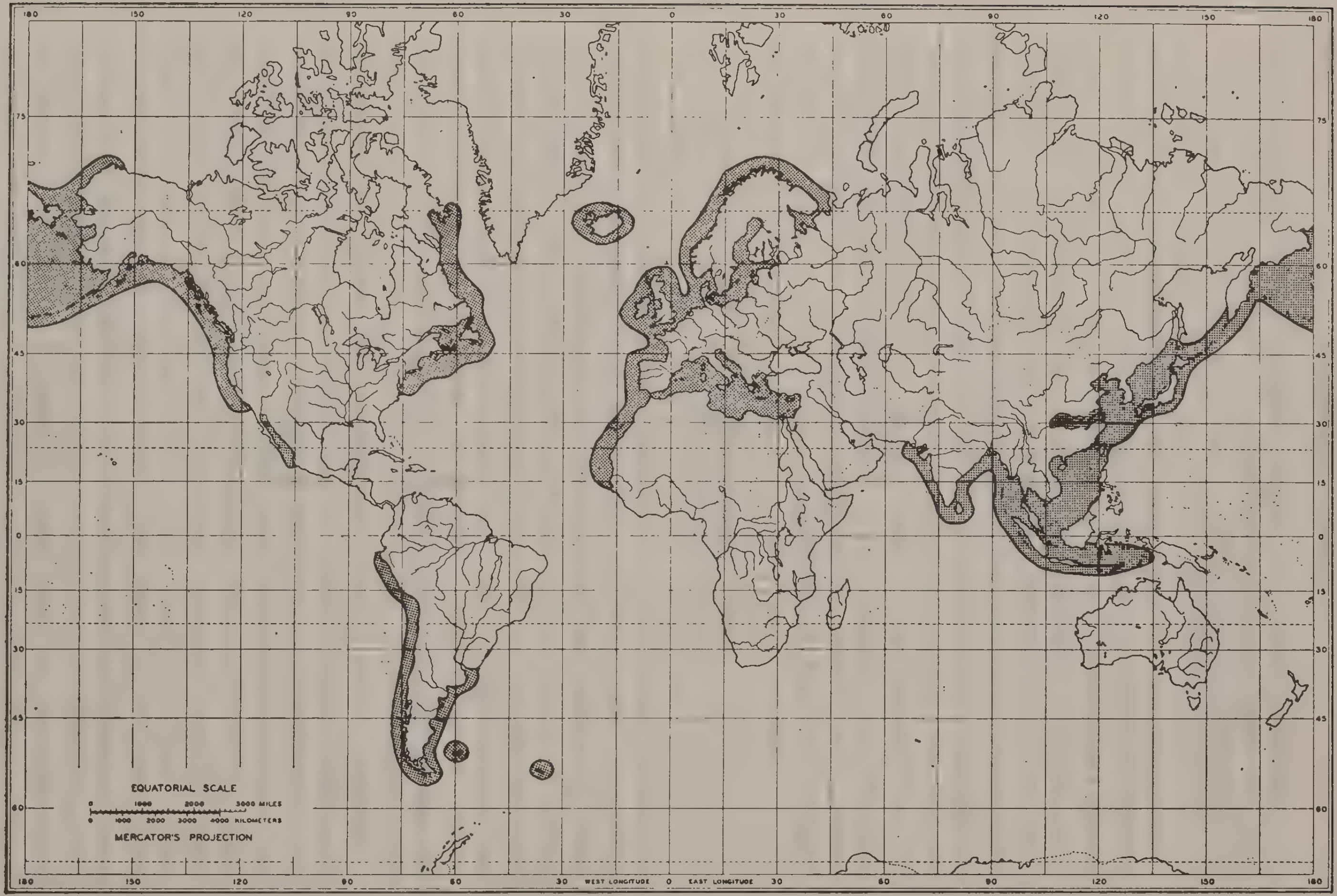
EQUATORIAL SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS
MERCATOR'S PROJECTION
WEST LONGITUDE
EAST LONGITUDE
180
150
120
90
60
30
0
75
45
15

Fig. 50. Distribution of Phocoenidae.

yellow, pink, or white, and others contrastingly marked in bold disruptive patterns of black and white; teeth from about 65/58 in *Delphinus capensis* to a minimum of 0/2 in adult *Grampus griseus;* teeth usually small and slender (thick and heavy in *Orcinus, Pseudorca,* and *Feresa*).

Habits. Dolphins are the most abundant and varied of cetaceans. Delphinids do not make deep or prolonged dives, but surface several times a minute. The small dolphins feed chiefly on small nektonic fishes and squids in the epipelagic zone of the open sea; some species feed on benthic and near-benthic fishes in shallow inshore waters, bays, and rivers. Pilot whales (*Globicephala*) and Risso's dolphins (*Grampus griseus*) are almost exclusively squid eaters; false killer whales (*Pseudorca crassidens*) feed on large pelagic fishes; and killer whales (*Orcinus orca*) prey on seals, dolphins, porpoises, whales, diving birds, sharks, large bony fishes such as salmon (*Oncorhynchus* spp.), and squids.

In the saddle-backed dolphin (*Delphinus delphis*), females apparently reach sexual maturity at an age of 3 years, males at 4 years; a female bottle-nosed dolphin (*Tursiops truncatus*), born in captivity, attained sexual maturity in 6 years; in pilot whales (*Globicephala melaena,* a polygynous species), females are sexually mature at 6 or 7 years, males not until about 12. In temperate latitudes, most delphinids breed during the summer months. Females usually ovulate only once during each reproductive cycle, but if they fail to become pregnant, they may ovulate two or even three times in succession. The ovaries are functionally asymmetrical; the left ovary matures earlier, and produces the majority of ovulations—58 to 83 per cent in the Orcininae, and 82 to 94 per cent in the Delphininae (condition in Cephalorhynchinae and Lissodelphinae not known). Female saddle-backed dolphins bear calves about three times in each 4 years, because of successive annual displacement of the time of parturition. Captive bottle-nosed dolphins have bred only in alternate years. In female pilot whales, the interval between successive calves is at least 3 years. The gestation period is 11 months in the saddle-backed dolphin, 12 months in the bottle-nosed dolphin, and 16 months in the pilot whale. Saddle-backed dolphin calves are weaned in 4 to 5 months. Captive bottle-nosed dolphin calves first take solid food at an age of about 6 months, but may continue to nurse until nearly 2 years old; the same situation seems to prevail among wild pilot whales. A climacteric apparently occurs in female pilot whales at an age of about 35 years, and in female saddle-backed dolphins at an age of about 20 years.

Maximum longevity is more than 20 years in the saddle-backed dolphin, about 50 years in the pilot whale. Most delphinids are gregarious; in the Black Sea, 100,000 saddle-backed dolphins have been observed in a single aggregation. Some species, such as pilot whales, appear to have a distinct social organization. Delphinids are swift and active, and frequently leap clear of the water; the spinner dolphins (*Stenella longirostris* and *S. roseiventris*) habitually execute one or two "barrel rolls" in mid-air; trained *Lagenorhynchus obliquidens* can clear a wire 4.8 m. above the water; some species habitually ride the bow waves of moving ships. Several of the smaller species of dolphins are taken commercially in large numbers in the Black Sea and around Japan; pilot whales are taken in Norway, Newfoundland, and the Lesser Antilles (Alpers, 1961; Essapian, 1962; Sergeant, 1962; Sleptsov, 1940, 1941; Tavolga and Essapian, 1957).

Habitat. Chiefly oceanic and neritic; *Orcaella* is also estuarine and fluviatile, and *Tursiops* inhabits fresh waters in the St. Johns River, Florida.

Recent Distribution. All oceans, and certain rivers of tropical southeastern Asia. Not mapped.

Recent Genera. (14, *ca.* 32 Recent species)

- Subfamily Orcininae
  - *Feresa* Gray, 1870 (1)
  - *Globicephala* Lesson, 1828 (2)
  - *Orcaella* Gray, 1866 (1)
  - *Orcinus* Fitzinger, 1860 (1) [= *Grampus auct., non* Gray, 1828]
  - *Peponocephala* Nishiwaki and Norris, 1966 (1) [= *Electra* Gray, 1866, *nec* Lamouroux, 1816]
  - *Pseudorca* Reinhardt, 1862 (1)
- Subfamily Lissodelphinae
  - *Lissodelphis* Gloger, 1841 (2)
- Subfamily Cephalorhynchinae
  - *Cephalorhynchus* Gray, 1846 (4)
- Subfamily Delphininae
  - *Delphinus* Linnaeus, 1758 (2)
  - *Grampus* Gray, 1828 (1) [= *Grampidelphis* Iredale and Troughton, 1933]
  - *Lagenodelphis* Fraser, 1956 (1)
  - *Lagenorhynchus* Gray, 1846 (6)
  - *Stenella* Gray, 1866 (7) [= *Prodelphinus* Gervais, 1880]
  - *Tursiops* Gervais, 1855 (2)

Geologic Range. Early Miocene to Recent in Europe and North America; Recent in all oceans.

Major Fossil Groups. More than 20 extinct genera have been described.

Remarks. This family was reviewed by True (1889) who, like many authors, broadened its scope to include what are here called the Monodontidae, Stenidae, and Phocoenidae.

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Calif. Fish and Game, 53 (1) : 35–39. 1967.

STEMONOSUDIS ROTHSCHILDI, A NEW PARALEPIDID FISH FROM THE CENTRAL PACIFIC

WILLIAM J. RICHARDS
U.S. Bureau of Commercial Fisheries
Tropical Atlantic Biological Laboratory [1]

A new species of paralepidid fish is described on the basis of a single specimen found in the stomach of a lancetfish (*Alepisaurus richardsoni* Bleeker). It is easily distinguished from other species of *Stemonosudis* on the basis of a long snout, a low number of dorsal and anal rays, and a striking color pattern.

The fish described here as a new species in the iniomous family Paralepididae was taken from the stomach of a Pacific lancetfish that was caught by longline in the central Pacific (Rothschild and Uchida, 1963), and supplied to me by Brian J. Rothschild, Bureau of Commercial Fisheries, Honolulu, Hawaii.

STEMONOSUDIS ROTHSCHILDI SP. NOV.

Holotype:

U. S. National Museum No. 199087, juvenile, 107 mm SL. From the stomach of a specimen of *Alepisaurus richardsoni* 460 mm SL, caught on longline gear from the U. S. Bureau of Commercial Fisheries R/V *Charles H. Gilbert* at lat. 22° 47′ N., long. 150° 09′ W. on February 15, 1963.

TABLE 1

Comparison of Morphological Characters of *S. rothschildi* and All Other Species of *Stemonosudis*

Character	*S. rothschildi*	All other *Stemonosudis* spp. (from Rofen, 1966)
Color:		
Dorsal blotches in advance of dorsal fin	5	0 to 3
Ventral blotches in advance of anal fin*	4	0 to 2
Vertical bands posterior to the dorsal fin	3	0 or 1
Meristic:		
Dorsal and anal rays	9 and 33	13 and 30 or 7 to 9 and 35 or more
Morphometric: (Percentage of standard length)		
Head length	20.6	14.7–18.3
Snout length	11.1	6.7–10.3
Premaxillary length	10.3	6.8– 9.6
Predorsal length	72.8	58.3–68.0
Distance between dorsal and anal fin	5.2	9.6–17.5

* These blotches are superficial and not to be confused with peritoneal pigmentation.

Diagnosis:

A *Stemonosudis* differing from the other species of the genus by a distinctive color pattern and several meristic and morphometric characters (Table 1).

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[1] Submitted for publication April 1966. Contribution No. 27, Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida.

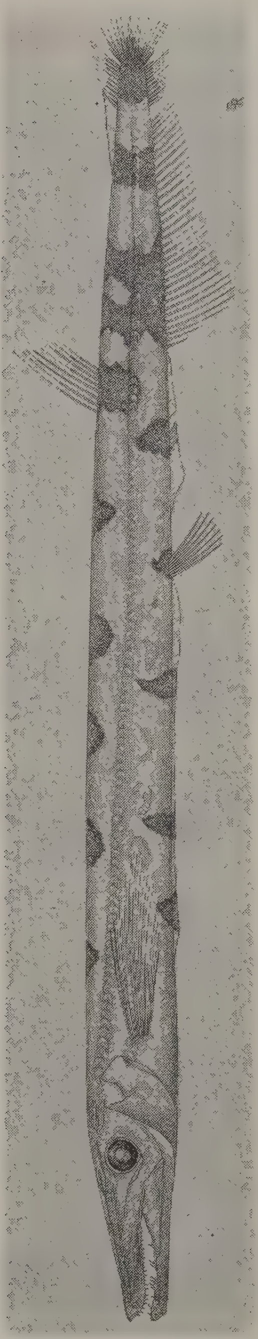

FIGURE 1—*Stemonosudis rothschildi,* holotype, USNM 199087, juvenile 107 mm SL. *Drawing by Grady Reinert.*

Counts and Measurements:

The specimen has several badly torn areas, and is twisted and distorted. Therefore, many of the measurements and the counts of the lateral-line sections and the vertebrae are unreliable. Dorsal rays 9 (all rays counted); anal rays 33 (all rays counted); pectoral rays 12 on each side; pelvic rays 8 on each side; approximately 109 scale-like lateral-line sections; approximately 90 vertebrae. Proportional measurements in thousandths of the standard length: body depth 61; caudal peduncle length 40; caudal peduncle depth 21; distance from snout to vent 617; head length 206; snout length 111; eye diameter 24; interorbital width 24; upper jaw length 103; predorsal length 728; length of dorsal fin base 30; pelvic fin origin to dorsal fin origin 148; dorsal fin origin to anal fin origin 52; tip of snout to origin of anal fin 742; length of anal fine base 176; pectoral fin length 145; prepelvic length 574; pelvic fin length 57; dorsal adipose fin origin to caudal base 62.

Description:

Lateral-line scales, body scales, and scale pockets not discerned. Lateral-line sections bony, typical of the genus. Ventral carina moderately developed; no dorsal carina visible. Two ventral adipose fins (may be remnants of a single damaged fin) in advance of anal fin; one dorsal adipose fin in advance of caudal fin.

Anterior portion of premaxillary bone with small hooked teeth curving posteriad; posterior portion with similar teeth curving mediad. Large, posteriorly curving, fang-like teeth on each side of palatine bones. Two large, fang-like replacing teeth ("depressible") prominent on each palatine bone. Each dentary bone with a single row of six erect fangs and an inner row of four replacing teeth ("depressible") curving posteriad. Tongue and prevomer toothless.

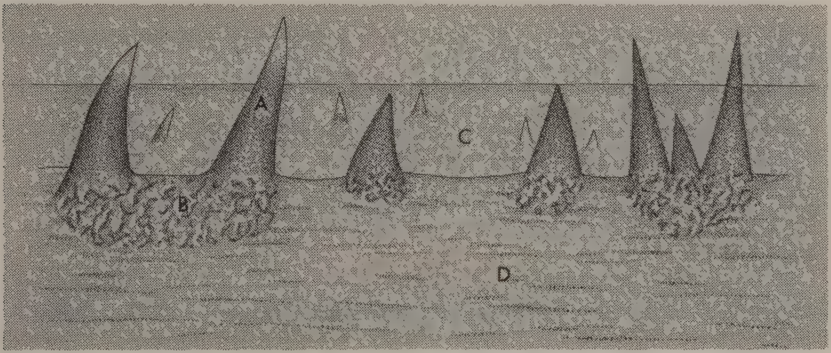

FIGURE 2—Section of the first gill arch of the holotype showing (A) gill tooth; (B) tooth platelet; (C) mucosa; and (D) gill arch. *Drawing by Grady Reinert.*

Gillrakers (gill teeth) in one row on gill arch, mostly in pairs; each pair on a separate tooth platelet (Figure 2B). Replacing gill teeth present in mucosa of a gill arch stained with Alizarin Red S (Figure 2); teeth stained deeply, but showing no apparent replacement pattern. Fixed teeth also stained deeply (Figure 2A) except at tips, in platelet (Figure 2B), and in gill arch.

Coloration:

The striking feature of this species is the bold, dark color pattern. Six dorsal and four ventral blotches anterior to the anal fin; and three wide bands (the anteriormost divided dorsally) posterior to the anal fin origin. These blotches and bands are formed by heavy concentrations of dark pigment near the surface of the skin. Seven or eight smaller peritoneal blotches lying deeply along ventral body wall. Damage to the specimen (not shown in Figure 1) prevents accurate determination of the number of these deep-lying blotches, or whether the third and fourth dorsal blotches are entire. Remainder of body clear except for very small scattered chromatophores in region of lateral line and near fin bases.

Pectoral fin rays with scattered chromatophores. Dense concentrations of chromatophores present on interradial membranes starting about ⅕ distally from base, but becoming faint on distal ⅕ of fin; thus, middle portion of fin very dark. Pelvic fin rays with dark chromatophores scattered along their entire length; interradial membranes with very dark concentrations of chromatophores throughout their length.

Anterior ventral adipose fin heavily scattered with dark chromatophores; posterior one clear. Dorsal adipose fin with heavily scattered, dark chromatophores.

Dorsal fin rays heavily pigmented with evenly spaced dark chromatophores; interradial membranes pigmented as with pelvic fins. Anal fin pigmentation similar to that of dorsal, but only 5th through 12th interradial membranes heavily pigmented. Caudal fin rays, broken off short in the specimen, with a few chromatophores on basal portions; none on remnants of distal portions.

Head with various-sized chromatophores most heavily concentrated on ridges and edges of bones of snout, on premaxillary bone, and over brain.

Species Associates:

Other fishes found in the lancetfish stomach with *S. rothschildi* include: one *Sternoptyx diaphana* Hermann, 20 mm SL; one *Pteraclis velifer* (Pallas), head missing; one *Ranzania laevis* (Pennant), 9.7 mm SL; and one post-larval flatfish (Heterosomata), 20 mm SL.

Relationships:

S. rothschildi is referred to *Stemonosudis* because it conforms to the following diagnostic characters of that genus (Harry, 1953*a*,*b*; Rofen, 1966): more than 24 anal rays; 84–121 vertebrae; short pectoral fin; naked head and body; snout to vent length 61.7% of standard length; elongate body; dorsal fin originating well behind middle of body; anterior lateral-line sections longer than high; and nostrils anterior to posterior tip of maxillary.

Knowledge of the species of *Stemonosudis* is so incomplete—a number of the species, including *S. rothschildi*, are known only from juvenile and/or larval stages—that comments on interspecific relationships are impractical. Superficially, at least, *S. rothschildi* does not seem to be closely related to any of the other species. The characters used here to separate *S. rothschildi* from the other species (Table 1) do not significantly change with age in those species which are known from comparable and smaller sizes (Marshall, 1955; Ege, 1957).

ACKNOWLEDGMENTS

J. Lockwood Chamberlin and Bruce B. Collette, Bureau of Commercial Fisheries, critically read the manuscript. Collette also provided the X-ray. Grady Reinert, Bureau of Commercial Fisheries, made the figure.

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86632—250 1-67 700

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pp. 245–247

FIRST ATLANTIC RECORDS OF THE NARROW-CORSELETED FRIGATE MACKEREL, *AUXIS THAZARD*.—The scombrid genus *Auxis* is distinctive in the combination of the following characters: dorsal fins broadly separated; dorsal finlets 8; anal finlets 7; interpelvic process single and long (equal to length of pelvic fins); body with a scaly corselet anteriorly, naked posteriorly. Fraser-Brunner (1950), Rivas (1951), and others concluded that *Auxis* contained only one species, *A. thazard* (Lacépède), which was reported as worldwide in tropic and subtropic seas. Fitch and Roedel (1963), however, have differentiated two frigate mackerels, the cosmopolitan wide-corseleted *Auxis rochei* (Risso) and the narrow-corseleted *A. thazard* for which they listed only Pacific localities. Collette and Gibbs (1963) recorded both species in their preliminary field guide to Indian Ocean scombrids and indicated that both probably occur in the Atlantic Ocean. Cervigón (1966) recorded and figured *A. thazard* from Venezuela, but he was not aware of the occurrence of two species in the region. In a recent letter to the junior author he indicated that he is almost certain that he confused the two species in the account for his book. However, the five specimens from the Porlamar fish market that he retained in his collection at the Estacion de Investigaciones Marinas de Margarita are all *thazard.* They are as follows: MHNLS 555 (3, 296–305 mm fork length); MHNLS 1925 (2, 315 and 324 mm). He gave the total gill-raker counts of these specimens as: 38, 41, 41, 42, and 43. He added that *Auxis* is very abundant at Isla de Margarita and surrounding areas.

The authors independently determined that *A. thazard* definitely occurs in the Atlantic. Prior to the examination of adult specimens, the senior author discovered that there are larval forms of two species of *Auxis* in the Atlantic. The three adults examined by him are as follows: a female from the eastern Atlantic west of Liberia (TABL 100372, 442 mm SL, R/V Geronimo station GE-5-124, 05°44′ N, 14°28.2′ W, 23 February 1965); a male from the Caribbean Sea west of St. Vincent (TABL 100373, 471 mm SL, R/V Undaunted station UN-2-114, 13°16′ N, 62°32′ W, 27 March 1966); a female from the Caribbean Sea off Caracas, Venezuela (TABL 100374, 426 mm SL, R/V Geronimo station GE-7-116, 10°47′ N, 67°03′ W, 24 March 1966). These three specimens agree with descriptions of the narrow-corseleted form found in the Pacific (*cf.* Matsumoto, 1960; Fitch and Roedel, 1963; Watanabe, 1964; Yoshida and Nakamura, 1965).

The junior author obtained two adult specimens in the southern Caribbean. One of 378 mm fork length was purchased in the fish market at Port-of-Spain, Trinidad on 6 May 1964. This fish was not preserved (its identity as a second species of *Auxis* from the Atlantic was then not suspected); however, a photograph was taken (herein reproduced as Fig. 1). The second specimen, 417 mm fork length, was purchased at the Porlamar fish market in Isla de Margarita, Venezuela on 24 January 1965. It is deposited at the Institute of Marine Biology, University of Puerto Rico, Mayaguez (UPR 2506). The identity as *thazard* was confirmed by Bruce B. Collette who studied the specimen.

The two species of *Auxis* may be differentiated as follows:

rochei

Posterior extension of scaly corselet along lateral line 6 or more scales in width beneath second dorsal fin origin.

Dorsum with vertical or near vertical dark bars.

Tip of pectoral fin does not reach a vertical at front of scaleless dorsal area.

thazard

Posterior extension of scaly corselet along lateral line 1–5 scales in width beneath second dorsal fin origin.

Dorsum with wavy dark bands most of which are oblique.

Tip of pectoral fin extends posterior to a vertical at front of scaleless dorsal area.

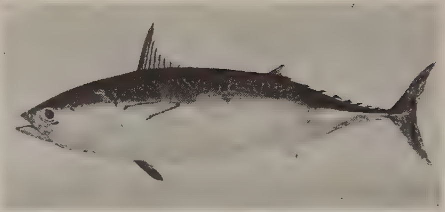

Fig. 1. *Auxis thazard* (378 mm fork length) purchased in the Port-of-Spain, Trinidad fish market on 6 May 1964.

In addition, the anterior processes of the haemal arches on the 24th to 28th vertebrae are better developed in *thazard* than in *rochei*, the body of *thazard* is more slab-sided, and *thazard* appears to have fewer gill-rakers, on the average. Our specimens had total gill-raker counts ranging from 37 to 43. Collette and Gibbs (1963) stated that *thazard* is reported to have a total of from 37 to 43 rakers and *rochei* from 40 to 47 in the Indian Ocean. Fitch and Roedel noted a higher gill-raker count for *thazard* in the eastern Pacific (41–47) than in the central and western Pacific (38–43). They indicated that the number of gill-rakers of *rochei* did not vary with area in the Pacific, but they did not give counts.

We propose the common name "bullet mackerel" for *Auxis rochei*.

This paper is contribution No. 47, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Fla.

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X^e Congrès européen sur les groupes sanguins
et le polymorphisme biochimique des animaux
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149, rue de Grenelle, Paris-7^e

A COMPLEX BLOOD GROUP SYSTEM IN SALMON AND TROUT

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SUMMARY

A twelve-factor system of blood groups was detected in sockeye salmon *(Oncorhynchus nerka)* and rainbow trout *(Salmo gairdneri)* with antisera prepared by isoimmunization of the rainbow trout. Statistical tests of independence, patterns of cross-reactivity, and preliminary genetic information from rainbow trout indicate that this is a complex multiple allelic system which resembles the B system of cattle and the Rh system of man.

INTRODUCTION

Research on blood groups of fishes has received emphasis during recent years because of the importance to management of distinguishing reproductively isolated populations of commercially valuable species. The field was recently reviewed by CUSHING, 1964. Species of Pacific salmon (genus *Oncorhynchus*) have particularly well-developed homing instincts; the physiology of their sexual maturation and the timing of their spawning migrations are precisely adapted to their natal streams. Consequently, these species are separated into many reproductively isolated populations. Analysis of these populations is thus a complex task dependent on accurate discrimination of genetically controlled differences. My associates and I began a program of isoimmunization of rainbow trout *(Salmo gairdneri)* several years ago to develop reagents for distinguishing blood groups in salmon and trout. Some of the results of our preliminary studies have been published, (RIDGWAY, 1962). In this paper I will describe more recent studies in which evidence has been obtained for the existence of a complex blood group system in sockeye salmon *(Oncorhynchus nerka)* and rainbow trout. Other workers have detected blood types in rainbow trout using antisera produced in rabbits (CALAPRICE and CUSHING, 1964; SANDERS and WRIGHT, 1962).

MATERIALS AND METHODS

Isoimmunization of trout :

Most of the work reported here was conducted on a group of 48 rainbow trout obtained from a commercial source. Their average weight was 500 gm when the isoimmunization program was started. All were held at the Hagerman National Fish Hatchery, U.S. Bureau of Sport Fisheries and Wildlife, Hagerman, Idaho. The water supply at this station comes from large springs which run at a nearly constant temperature of 15° C. The trout were fed a dry pelleted trout food which was supplemented with weekly rations of ground fresh beef liver.

The trout were immunized in pairs, each member of the pair serving as both donor and recipient. All bleedings were made by cardiac puncture of fish anesthesized with tricaine methane sulfonate (1:20,000). All injections were made intraperitoneally and consisted of 0.5 ml of freshly drawn whole blood containing 0.1 ml Alsever's solution as anticoagulant. Two immunization programs were used; one group of trout received three injections per week for three weeks, then one injection per week for five weeks; the other group received one injection per week for eight weeks. Better results were obtained with the group receiving weekly injections. Test bleedings of 2 ml were taken after six weeks of injections; those trout which had produced detectable isoimmune antibodies were bled 6 to 15 ml every 2 to 4 weeks thereafter.

Typing procedure :

All typing was done by the capillary agglutination method of Chown and Lewis (1946) using equal amounts of serum and 20 % suspensions of red cells in Alsever's solution. All cell suspensions were kept on ice until used. Readings were taken 10 and 30 minutes after setting up the capillary tubes. Those bleedings, from individual trout, that demonstrated identical reactions when tested with a panel of cells from 25 or more trout, including the surviving donors, were combined to produce pools of 20 to 200 ml.

Absorptions :

Absorptions were conducted by incubating one volume of washed and packed red cells with two volumes of serum for 1/2 hour at 20° C and one hour at 4° C. Most absorptions were made with erythrocytes of sockeye salmon taken from various streams in Alaska, Washington State and British Columbia. Usually this procedure was repeated to insure complete absorption.

RESULTS

My associates and I have used pooled isoimmune sera from 35 trout in extensive tests on several thousand sockeye salmon and rainbow trout. I will report here some results obtained with 12 of these sera whose specifications were found to be related. We named these reagents anti-A, -B, -C, -D, -E, -F, -G, -H, -J, -K, -L and -M.

Chi-square tests of independence on the results of typing sockeye salmon from several populations first indicated the relationship among these sera. Other evidence for their relationship has been obtained from preliminary genetic studies on rainbow trout, and from the phenogroup patterns obtained from the tests on sockeye salmon. Because of the similarity of these phenogroup patterns to some of those in the cattle B system, I have called the system in salmon and trout the B system.

The results we obtained on typing many populations of sockeye salmon show a significant lack of independence in the distribution of reactions with these sera. I will present two examples. Reagents A, B, C, D, E, F, H, J, L, K and M were used to test 39 sockeye salmon from the Skeena River in British Columbia, Canada. Reagent pairs whose reactions showed significant lack of independence, and their chi-square values are the following: AB 14.4, AD 10.8, AJ 4.1, BD 9.2, CD 7.25, DJ 3.9, EK 14.8, FH 6.0, FJ 4.3, FK 4.9, FM 4.75 and HJ 8.1. Reagents A, B, C, E, F, H, J, K, L, M were used to test 1,500 sockeye salmon from the Copper River in Alaska. Reagent pairs whose reactions departed significantly from independence and their chi-square values are the following: AB 11.5, AE 8.5, AJ 13.2, BH 9.7, BJ 6.0, CH 13.3, CM 9.8, EF 6.3, FL 6.2, HJ 6.3, HL 9.4, HM 7.6, JL 11.3 and LM 4.3.

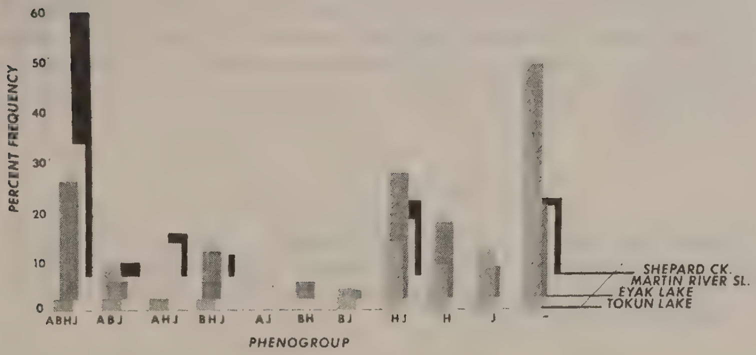

Fig. 1.
Frequencies of B system phenogroups in sockeye salmon populations from tributary areas of the Copper River in Alaska. For simplicity, only factors A, B, H and J are considered.

The results of our absorption experiments indicate that these reagents possess related, overlapping specificities and that they distinguish sets of related antigens. Some of the sets of reactions which occurred frequently in our study of sockeye salmon from the Copper River are: ABFHJ, ABHJK, CHJ, CHJM, FHJK, FHJLM, HJK, HJ, J, K, L, M, and "-" ("-" indicates no reaction with the 9 B system reagents used). We distinguished a total of 122 B system phenotypes in this study and found significant differences between tributary areas. Examples of differences in frequencies of phenogroups among sockeye salmon populations from tributaries of the Copper River are illustrated in Figure 1. For simplicity, only factors A, B, H and J are considered in this figure. Preliminary genetic studies with rainbow trout indicate that the antigenic specificities distinguished by these sera are inherited in groups. Some examples of the groups in trout are: ABDHJM, CGJ, CHJ, HJ, DL and D.

DISCUSSION

The resemblance of the "phenogroup" patterns in this blood group system of salmonid fish to those in the B system of cattle (or the Rh system of man, the B system of chickens, etc.) may seem remarkable at first thought. However, as STORMONT (1955) has pointed out, such patterns are the direct consequence of the nature of cross-reactivity obtained with a complex series of related antigens and antibodies. I expect the complexity of this sytem to increase, because we have many additional sera, not yet adequately studied to warrant inclusion in the system, that show significant relationship to the B system reagents.

The accuracy of typing animals like sockeye salmon, which are caught in wild areas and killed in the process of capture, is an important one. If one makes a mistake he cannot return and take another sample of blood from the same individual. We have examined this problem with rainbow trout held in captivity and found our results are reproducible with better than 95 per cent accuracy. We have also attempted to develop more sensitive testing methods. Serious and unsolved problems in applying both hemolytic and antiglobulin techniques have been encountered. Despite these problems, this system has proven useful for studying populations of salmon, and with further analysis may be important to the study of genetic and evolutionary questions in salmon, trout, and other fishes.

ACKNOWLEDGMENTS

This work was conducted at the Biological Laboratory, United States Bureau of Commercial Fisheries, Seattle, Washington. I gratefully acknowledge the assistance of R. SMITH, E. LARSON and R. CARTER with the isoimmunization program and the assistance of W. AMES, F. UTTER and H. HODGINS with the blood typing tests.

RÉSUMÉ

On a pu détecter un système de groupes sanguins à 12 facteurs chez *Oncorhynchus nerka* (variété de saumon) et *Salmo gairdneri* (truite arc-en-ciel) grâce à des antisérums préparés par iso-immunisation de la truite arc-en-ciel.

Des tests statistiques d'indépendance, les données de réactions croisées et des renseignements génétiques préliminaires sur la truite indiquent qu'il s'agit d'un système multiallélique complexe qui ressemble au système B bovin et au système Rhésus humain.

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DISCUSSION

J. S. ALABASTER: I would like to comment that we have also found that rabbit anti-salmon reagents are not very specific, neither are chicken anti-salmon reagents. We too have therefore turned to isoimmunization using salmon *(Salmo salar)* and also sea-trout *(Salmo loutta)* both of which appear to produce much more promising reagents.

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THE LOCOMOTION AND BEHAVIOR OF SURF CLAMS, *SPISULA SOLIDISSIMA*

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ABSTRACT

The locomotion and behavior of surf clams, *Spisula solidissima,* were investigated to assess their possible migratory abilities. Both field and laboratory observations were included in the study.

Observations were made on beach and offshore populations of surf clams. On beaches juvenile clams 20 to 70 mm in shell length displayed four types of activity: (1) gliding through the water (2) exhuming themselves from the exposed beach at low tide, (3) rapidly burrowing into the substrate as the tide flooded in, and (4) crawling over the substrate. These observations suggested that small clams may shift location, especially if bottom currents are present to carry the clams once locomotion is initiated. In the laboratory, juvenile clams propelled themselves off the bottom by muscular movements of the foot and glided a distance of 8 to 12 inches.

Low water temperatures resulted in reduced activity. Clams in the laboratory acclimated to a 10°C increase from 8°C within 24 hours and burrowed more rapidly than clams under the influence of low seasonal temperatures. A 22°C rise from 8°C caused gaping, lethargy, and eventual death. Clams were frequently observed emerging from exposed sand at low tide, but this activity has not been duplicated in the laboratory either by draining the water from the aquaria sand, heating the sand surface, or applying a weight to the sand surface. Crawling, by alternately penetrating the tip of the extended foot in the sand and contracting it, has been observed only infrequently in either the field or laboratory.

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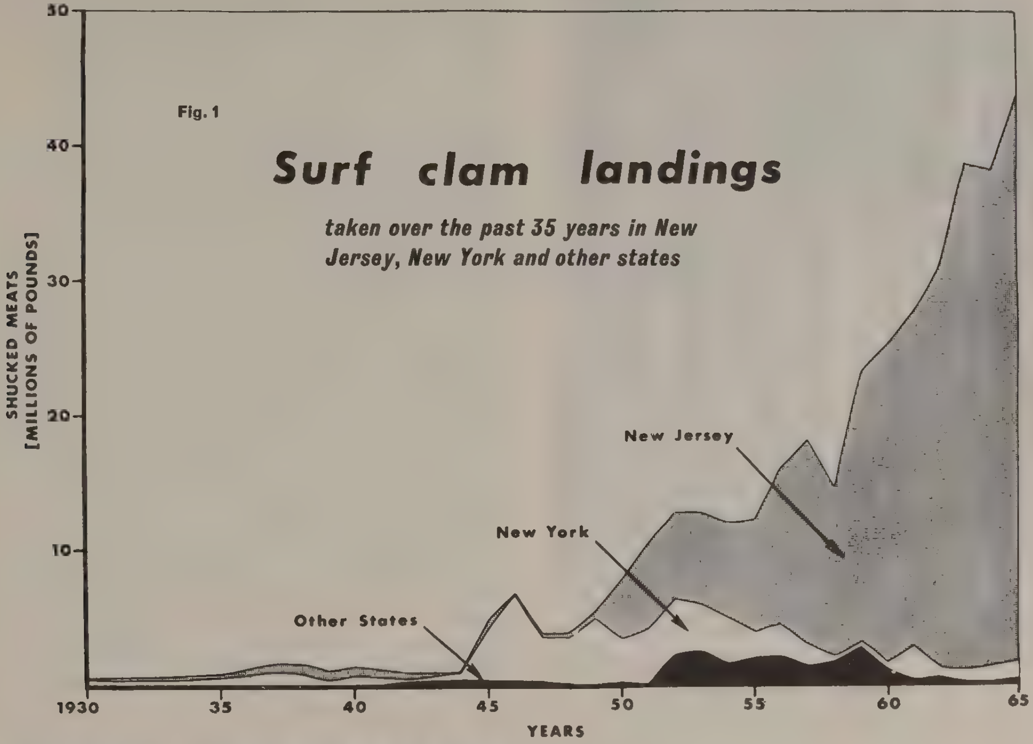


Fig. 1

Surf clam landings

taken over the past 35 years in New Jersey, New York and other states

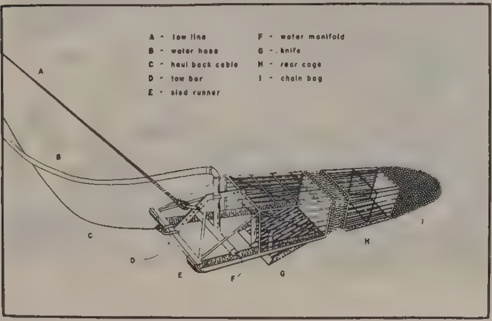
SURF CLAMMING – a growing fishery

BY

JOHN W. ROPES, *US Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland.*

MANY bivalve mollusks inhabiting the western North Atlantic coast have been used for food since Colonial days. Today five species are sources for major fisheries in the eastern United States: the surf clam (*Spisula solidissima*), the sea scallop (*Placopecten magellanicus*), the soft-shell clam (*Mya aernaria*), the oyster (*Crassostrea virginica*), and the northern hard clam or quahog (*Mercenaria mercenaria*). Other species of bivalves support minor fisheries: the southern hard clam (*Mercenaria campechiensis*), the ocean quahog (*Arctica islandica*), the bay scallop (*Aequipecten irradians*), the calico scallop (*Aequipecten gibbus*), and the blue mussel (*Mytilus edulius*).

Fig. 2. A schematic drawing of a surf clam jet dredge.



The surf clam supports the most recent and rapidly growing addition to our east coast shell fisheries; it has risen to a position of major importance within the past 20 years, over which period the total landings have increased almost 30-fold (Fig. 1). Large surf clams are found from Nova Scotia to North Carolina but are most abundant along the middle Atlantic coast from shore to depths of about 120 ft. Surf clams are the largest bivalves caught in coastal waters of the eastern US; some grow to eight inches, although most clams caught in the fishery

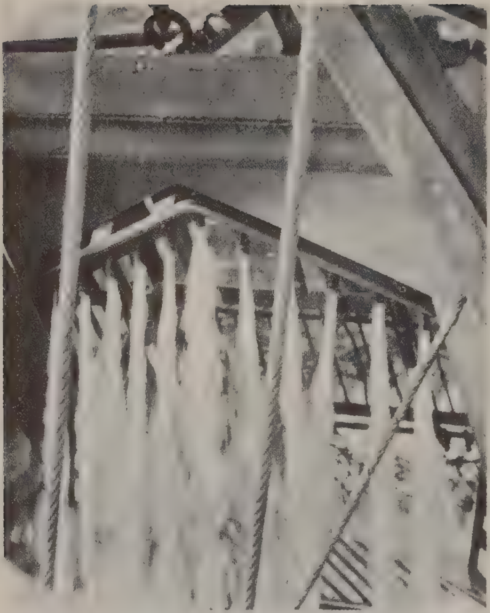


Fig. 3. The bottom view of a jet dredge hanging alongside the vessel. Jets of water are being pumped out of the nozzles and between the 10 in. wide runners.

are five to six inches long. They usually live buried in sandy bottoms to depths about equal to their shell length. Other common names for the surf clam are skimmer clam, bar clam, hen clam, and sea clam.

The coastal waters of six states — Massachusetts, Rhode Island, New York, New Jersey, Delaware, and Maryland — contribute to the yearly landings of surf clams (Fig. 1). Before 1945 the fishermen had inefficient dredges that broke many clams; consequently only small quantities were landed. Most of these clams were mixed with sand and suitable only for bait.

An increase in consumer demand for clam products after World War II soon caused the need for surf clams to exceed the landings. Then the hydraulic dredge (Fig. 2), developed on Long Island, NY in late 1945, became a practical, efficient tool for catching clams. Almost immediately landings increased. The Long Island offshore beds produced 6.5 million lb. of surf clams meat in 1946, as compared with a catch of 1.2 million lb. in 1944. Extensive beds were discovered off the New Jersey coast in 1950; landings from these beds have surpassed any previous record. In 1965, total landings reached a peak of 44.1 million lb. of meats, valued at US $3.2 million; more than 42 million lb. of the total were landed at New Jersey ports.

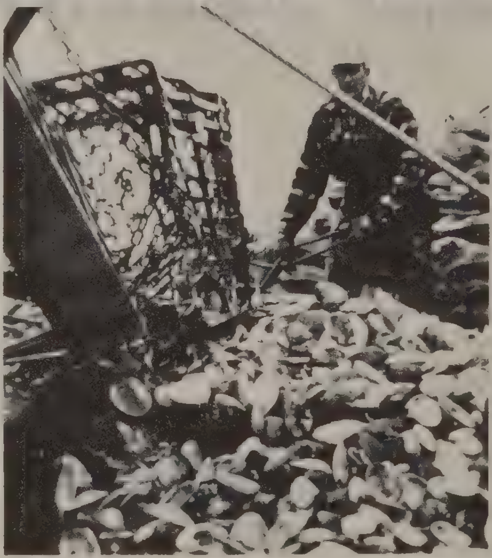
The surf clam vessels that today dock mostly at Pt. Pleasant, Wildwood, and Cape May, NJ, are of various designs: shrimp trawlers, small inshore draggers, oyster dredge vessels, and surplus military vessels. Characteristically, these 65- to 90-ft. long vessels have a spacious deck for stacking a day's catch of surf clams and storing the hydraulic dredge and auxiliary equipment. Dredges on these vessels commonly weigh about one ton, although lighter and heavier ones are used. Surf clam vessels usually have at least two power plants — one to propel the vessel and operate the winch when fishing, and another to drive the pump for the dredge's hydraulic system.

The distinctive features of hydraulic surf clam dredges include jets of water to loosen the sand ahead of the digging blade and to wash clams into the dredge (Fig. 3). The dredge digs into the bottom throughout a tow, breaks very few clams, and is hauled aboard for unloading the accumulated catch. Surf clam dredges have been fished experimentally in depths of 250 ft.

A description of a day's trip on a vessel equipped with the hydraulic surf clam dredge illustrates the efficiency of this clamming method. Provided the sea is not too rough, the trip begins before sunrise, and the vessel arrives at the fishing grounds after one or two hours. A two- or three-man deck crew casts the tow line and six-inch diameter hose overboard while the skipper turns the vessel in a wide circle to prevent fouling the propeller. The hose inflated by air floats at the surface and trails aft from the pump to the hydraulic manifold of the dredge. The tow line, attached to an aftermast A-frame on oyster vessels or a kingpost on other vessels, trails aft to the towing bar on the dredge.

In rapid sequence, the dredge is put overboard, the pump engine is started, a nearby gate valve is opened, and water flows through the hose to spray out of the nozzles on the jet manifold. Almost simultaneously with the opening of the gate valve, the winch brake is released and the dredge falls to the bottom. The cable runs out freely until the tow line tightens to begin a drag. An elastic tow line, such as polypropylene, is used for dragging, instead of the steel cable, to reduce chances of losing

Fig. 4. Tying the dredge ring bag after dumping the load on deck.



the dredge if it anchors in the bottom. The cable is used only to lower and retrieve the dredge. An experienced crew can begin fishing with the dredge about 15 minutes after arriving at a site.

The vessels make repeated tows at a site; they average four tows an hour, and seek catches of 10 to 15 bushels a tow. If catches are less than seven bushels a tow, they move to another spot. Catches have been as large as 42 bushels, or about two tons, but if the catch approaches this amount, the duration of tow is reduced to prevent strain and damage to cable and dredge. The dredge is hoisted up over the deck, the catch released (Fig. 4), the purse line tied, and the dredge put back over the side.

The deck crew then begins to select large, four- to seven-inch clams from the pile. On most vessels, the clams are placed into a funnel-like, bottomless hopper that has been stuffed into the opening of a heavy burlap bag. When the hopper is full, a fisherman lifts it to slide the clams into the bag; the bags are stacked on deck.

Varying amounts of debris, such as clam shells, conchs, horseshoe crabs, sea cucumbers, starfish, stones, and pieces of wood are shovelled overboard. An experienced skipper seeks fishing sites that yield most surf clams; surprisingly little shovelling is necessary after such tows.

The vessels return to port after eight to 12 hours at sea, although the time actually spent dredging is usually six to nine hours. An average day's catch is 350 bushels, but twice that amount may be caught if a particularly productive area is found. Sometimes such an area is very restricted, and several vessels will work it together. More often, however, each vessel fishes alone, and buoys are set to mark a good site for repeated trips.

At the dock, six bags or one cage of clams at a time are lifted into trucks for shipment to shucking plants; some go directly to dockside plants. A day's work often ends late at night.

The clams are stored overnight in cool rooms; processing begins early in the morning. Shuckers stand at a long table to receive the clams. They cut the muscles holding the shells of a clam together, one shell is flipped off, and the meat scooped out into a stainless steel container. Full containers are moved to another area in the building where workers separate and discard the large visceral mass that contains the digestive tract, reproductive organs, heart, and liver. Thus, in surf clams, unlike most other edible bivalves, only the muscle is retained for food. Thorough washing and inspection accompany the processing to remove sand and bits of shell.

This fishery is young, vital, and dynamic. At the request of the surf clam industry, scientists of the US Bureau of Commercial Fisheries Biological Laboratory at Oxford, Md., and Exploratory Fishing and Gear Research Base at Gloucester, Mass., are studying the biology of the surf clam and its distribution and abundance in the sea. Intelligent management of the resource depends upon such fundamental studies if clams are to be available for future generations.

123

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Vol. 81 October, 1967 No. 2

MALACOBDELLA GROSSA IN PITAR MORRHUANA AND MERCENARIA CAMPECHIENSIS

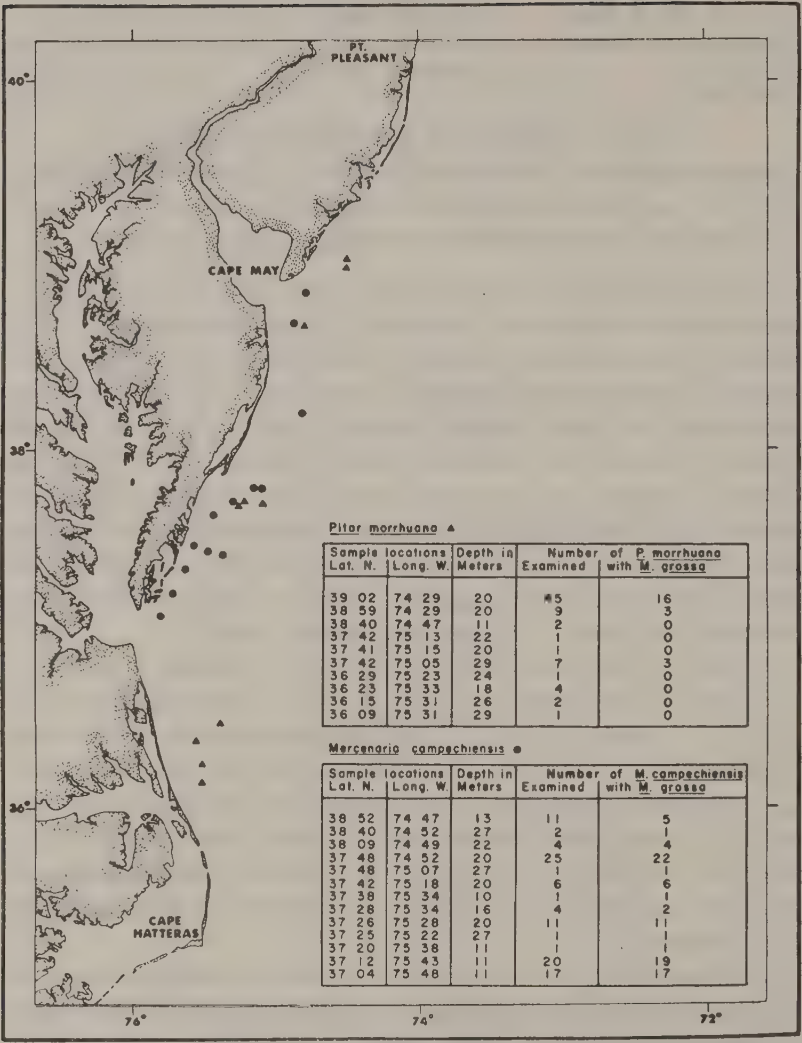
By JOHN W. ROPES AND ARTHUR S. MERRILL
U. S. Bureau of Commercial Fisheries Biological Laboratory, Oxford, Md.

Specimens of the morrhua venus, *Pitar morrhuana* (Linsley), containing the commensal nemertean, *Malacobdella grossa* (O. F. Müller), were collected during a May-June 1966 cruise of the Bureau of Commercial Fisheries research vessel "Delaware." *Pitar morrhuana* has been recently discovered as a fifth host for the nemertean along the western North Atlantic coast by Ropes (1966). The present account adds to the records of the initial discovery and includes observations of the nemertean in the southern quahog, *Mercenaria campechiensis* (Gmelin). More extensive distributional records of the quahog offshore of the middle Atlantic coast were reported by Merrill and Ropes (1967).

A hydraulic surf clam dredge caught 73 *P. morrhuana* at 10 of 447 locations from Montauk Point, N. Y., to Ocracoke Inlet, N. C. (Fig. 1). A total of 61 *P. morrhuana* came from three locations; 22 contained the nemertean, an incidence of 36%. None of the remaining 12 clams, from seven other locations, contained the nemertean. The shell length measurements of the clams ranged from 18 to 50 mm. and averaged 35.9 mm.; *M. grossa* occurred in specimens 27 to 47 mm. long. No multiple occurrences of the nemertean were observed.

The nemertean was found in 91 of 104 *M. campechiensis* from 13 locations (Fig. 1), an incidence of 87.5%. Porter (1962) found the nemertean nearly as often (83.3%) in southern quahogs taken off North Carolina. We found multiple occurrences in two clams; one contained 4 worms, the other 2. The quahogs were larger (length range, 80 to 127 mm.; average, 104.5 mm.) than *P. morrhuana* — providing more space for multiple occurrances of the nemertean. Generally, only one nemertean inhabits each host.

Martin L. H. Thomas, Fisheries Research Board of Canada, Biological Substation, Ellerslie, P. E. I., found *M. grossa* in *P. morrhuana* from the Gulf of St. Lawrence north to Goose Harbor,



Pitar morrhuana ▲

Sample locations Lat. N.	Sample locations Long. W.	Depth in Meters	Number of *P. morrhuana* Examined	Number of *P. morrhuana* with *M. grossa*
39 02	74 29	20	[illegible]5	16
38 59	74 29	20	9	3
38 40	74 47	11	2	0
37 42	75 13	22	1	0
37 41	75 15	20	1	0
37 42	75 05	29	7	3
36 29	75 23	24	1	0
36 23	75 33	18	4	0
36 15	75 31	26	2	0
36 09	75 31	29	1	0

Mercenaria campechiensis ●

Sample locations Lat. N.	Sample locations Long. W.	Depth in Meters	Number of *M. campechiensis* Examined	Number of *M. campechiensis* with *M. grossa*
38 52	74 47	13	11	5
38 40	74 52	27	2	1
38 09	74 49	22	4	4
37 48	74 52	20	25	22
37 48	75 07	27	1	1
37 42	75 18	20	6	6
37 38	75 34	10	1	1
37 28	75 34	16	4	2
37 26	75 28	20	11	11
37 25	75 22	27	1	1
37 20	75 38	11	1	1
37 12	75 43	11	20	19
37 04	75 48	11	17	17

Figure 1. Sample locations for *Pitar morrhuana* and *Mercenaria campechiensis* and numbers containing *Malacobdella grossa,* middle Atlantic coast.

P. E. I., and Grand Etang, Nova Scotia (personal communication). Of 15 *P. morrhuana* collected from Malpeque Bay on 25 August 1966, 12 (35 to 50 mm. long) contained the nemertean.

Coe (1954) reported that *M. grossa* is widely distributed along the Atlantic coast from Nova Scotia to Texas. Ropes (1966) found the association of the commensal and *P. morrhuana* in offshore New Jersey waters. The above records extend the geographical

Table 1. A list of known mollusk hosts for the genus Malacobdella

Atlantic coast pelecypod hosts for *Malacobdella grossa*	Reference
Mercenaria mercenaria	Coe, 1943
Mercenaria campechiensis	Porter, 1962
Crassostrea virginica	Coe, 1943
Mya arenaria	Coe, 1943
Pitar morrhuana	Ropes, 1966; M.L. H.Thomas, 1967 (Personal Communication)
European coast pelecypod hosts for *Malacobdella grossa*	
Mya arenaria	Coe, 1943
Mya truncata	" "
Cardium aculeatum	" "
Isocardia cor	" "
Venus mercenaria	" "
Pholas crispata	" "
Arctica islandica	" "
Mactra stultorum	" ".
Pacific coast pelecypod hosts for *Malacobdella grossa*	
Siliqua patula	Guberlet, 1925
Macoma secta	Coe, 1943
Pacific coast pelecypod hosts for *Malacobdella minuta*	
Yoldia cooperi	Coe, 1945
Japanese coast pelecypod hosts for *Malacobdella japonica*	
Mactra sachalinensis	Takakura, 1897
South American gastropod hosts for *Malacobdella auriculae*	
Chilina dombeiana	Guberlet, 1925

range of this association north to the Gulf of St. Lawrence and south to below Chesapeake Bay. The nemertean association with *M. campechiensis* described above extends the records of this relationship north to Cape May, N. J. Porter (1962) originally found the nemertean in southern quahogs off Cape Lookout and Beaufort, N. C. Since *M. campechiensis* occurs southward into the

Gulf of Mexico (Abbott, 1954), possibly the nemertean is present in these clams too.

Seventeen molluscan species serve as hosts for the genus *Malacobdella* (Table 1); and 14 of these are listed for *M. grossa.* Two species of the genus *Mactra,* taxonomically close relatives of surf clams, *Spisula solidissima* (Dillwyn), are hosts for the nemertean—one on the European coast and one on the Japanese coast. Although the relationship between *M. grossa* and the two species of *Mactra* suggests that the nemertean might occur in surf clams, none of several thousand clams opened in our studies has contained it. Numerous ocean quahogs, *Arctica islandica* (Linnaeus), a host for the commensal in Europe (Brunberg, 1964), have also been examined with negative results. Both *S. solidissima* and *A. islandica* are more abundant and widely distributed than *P. morrhuana* and *M. campechiensis* along the middle Atlantic coast. Nevertheless, apparently the nemertean is unable to associate with either of the species.

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MARKING SURF CLAMS FOR GROWTH STUDIES

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ABSTRACT

Various marking techniques were tested on surf clams, *Spisula solidissima,* as part of studies on population dynamics and growth. The methods of collecting large numbers of juvenile surf clams at Chincoteague Inlet, Virginia, in late 1964, applying colored liquids to the shells, attaching plastic discs and tapes to the shells with adhesives, and grinding notches in the shells are described.

The colored liquids were generally unsatisfactory marks on recovered clams. Notches clearly delimited increments of new shell growth. New adhesives appear to be promising as a means of attaching colorful individual markers and can be used in conjunction with shell notches for planting in the offshore fishery. The colorful marker improves the chance of recovering notched clams by attracting the attention of the fishermen.

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THE GROWTH OF JUVENILE SURF CLAMS AT CHINCOTEAGUE INLET, VIRGINIA

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ABSTRACT

Juvenile surf clams, *Spisula solidissima*, were collected, marked, planted, and recovered over an 18 month period in Chincoteague Inlet, Virginia, to obtain measurements of growth. A notch ground into the shell margin was used as a reference mark of the clam's original shell length when planted.

Clams from the Chincoteague Point planting site grew an average of 42.1 mm in length after 18 months or about 2.4 mm per month. Slower growth (22.7 mm after 18 months or 1.3 mm per month), apparently due to unfavorable environmental conditions, was observed at the Assateague Cove planting site. Unmarked clams from Wallops Island increased in length from 21.1 mm to 66.2 mm in 18 months, an average of 2.5 mm per month. An analysis of variance showed no significant difference between the growth of marked clams from Chincoteague Point and unmarked clams from Wallops Island. Thus, notching the shell margin of surf clams appears to be a useful method of providing accurate measurements of growth.

Competition for Gear in a Multiple-Species Fishery

By

Brian J. Rothschild

Competition for Gear in a Multiple-Species Fishery

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The catch-per-unit-of-effort (CPUE) for one species may affect the CPUE of another species in a multiple-species fishery. This effect is studied by means of a simple stochastic model. The model provides a "competition free" CPUE which is never less than the CPUE obtained under competition, is strongly dependent on the empty space on or in the gear, and varies as a function of the proportion of each species. The multinomial structure of the model enabled the derivation of maximum-likelihood estimators of its parameters. Estimates of the large sample sampling variances and covariance of the parameters are also provided. Application of concepts of the model to other fishery problems is discussed and it is noted that the model also provides a maximum-likelihood estimate for the well-known yield equation.

Introduction

Many fisheries simultaneously harvest several species of fish. The unit of effort expended in a multiple-species fishery is usually applied to the catch of each species in that fishery. Thus, if 20 units of effort are expended to catch, simultaneously, 10 fish of species 1, and 30 fish of species 2, the catch-per-unit of-effort (CPUE) would be computed as 0·5 and 1·5, respectively. The possibility that the several species taken in a fishery compete for "space" on or in the gear has been infrequently acknowledged; see, however, Ketchen (1964) and Gulland (1964). Under the postulate of competition for space on or in the gear, the above values of 0·5 and 1·5 would be underestimates of the CPUE as an index of density for each species independent of the presence of other species. This paper considers the concept of competition for gear by more than one species. The consideration is based on a simple model contrived to demonstrate the concept.

Model

The model exploits the analytical simplicity of the known number of hooks on a longline-type of gear. Gulland (1955) and Murphy (1960) also took advantage of this feature to formulate models for gear competition. In our

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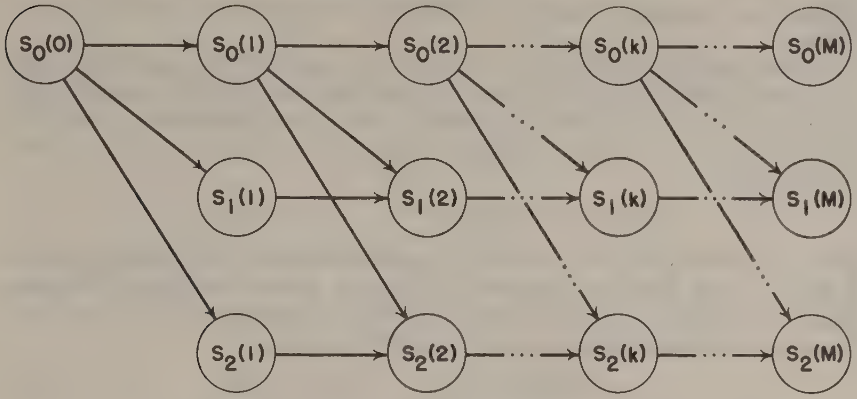

Figure 1. Diagram of possible routes of passage among the states for successive instants of time.

model a single, individual hook is placed in the water and examined for $k = 1, 2, \ldots, M$ successive instants of time (in reality, however, we can only examine the hook when we remove it from the water at the end of the M-th instant of time). During each instant the hook can remain empty, catch species 1, or catch species 2. Furthermore, we assume that the hook can remain empty for all instants of time, but if species 1 takes the hook it remains on that hook until the end of the M-th instant, and likewise for species 2. The events that the hook is empty in any instant, contains species 1, or contains species 2 are denoted as states S_0, S_1, S_2, respectively. This set of rules, which delimits the possible routes of passage among the states through the successive instants of time, is diagrammed in Figure 1. The probabilities of $S_i(k-1)$ passing to $S_j(k)$ are q_{ij}, which for any i, j is constant for all k. In this particular model $q_{00} > 0$, $q_{01} > 0$, $q_{02} > 0$, $q_{11} = 1$, $q_{22} = 1$, all other $q_{ij} = 0$.

We define the probability that the system is in the i-th state at time M as Q_i,

$$P[S_i(M)] = Q_i, \qquad i = 0, 1, 2 \tag{1}$$

The probabilities Q_i can be estimated from a set of independent hooks (a collection of hooks such that the probability of any hook containing a fish is unchanged by the event that any other hook in the collection contains a fish). The question of independence among hooks was considered by Maéda (1960) and Murphy and Elliot (1954). As the hooks are removed from the water at the end of the M-th instant, the number that are empty (n_0), the number containing species 1 (n_1), and the number containing species 2 (n_2) provide an estimate of Q_i, *viz*: $\hat{Q}_i = n_i/N$, where $N = \Sigma n_i$. Note that 100 $\hat{Q}_1$ or 100 $\hat{Q}_2$ is the familiarly reported catch per hundred hooks of the Japanese longline fishery.

The Q_i ($i = 1, 2$), then, are the probabilities (and also CPUE for the longline fishery) of species i being on the hook in the presence of the possibility that species j could have occupied the hook instead. We now wish to derive from the Q_i's the probability of taking species i in an artificial situation where species j does not exist. This is analogous to the competing-risk-of-death problem, an elementary exposition of which the reader will find in NEYMAN (1950).

To treat species i independent of species j we imagine, in considering i, that every time species j takes the hook the fish becomes invisible, thus allowing the hook to remain available to species i. All other things being equal, the probability of species i being caught under the fictional condition where species j is absent is,

$$P_{0i} = 1 - (1 - q_{0i})^M, \qquad i = 1, 2.$$

Before we can relate the P_{0i} to the Q_i, however, each must be defined in terms of the q_{ij}. Note that the probability of neither species being caught in any instant is $1 - (q_{01} + q_{02})$, and therefore the probability that the hook will contain neither species at the end of the M-th instant is,

$$P\,[S_0(M)] = Q_0 = (1 - q_{01} - q_{02})^M. \tag{2}$$

The event that species 1 is on the hook at the M-th instant is

$$\begin{aligned} S_1(M) \equiv {} & [S_1(1) \cap S_1(2) \cap \cdots \cap S_1(M)] \cup \\ & [S_0(1) \cap S_1(2) \cap \cdots \cap S_1(M)] \cup \cdots \\ & \cup [S_0(1) \cap S_0(2) \cap \cdots \cap S_0(M-1) \cap S_1(M)]. \end{aligned} \tag{3}$$

Therefore,

$$\begin{aligned} P[S_1(M)] = Q_1 &= q_{01} + \sum_{k=2}^{M} (1 - q_{01} - q_{02})^{k-1} q_{01} \\ &= \frac{q_{01}}{q_{01} + q_{02}} [1 - (1 - q_{01} - q_{02})^M] \\ &= \frac{q_{01}}{q_{01} + q_{02}} (1 - Q_0). \end{aligned} \tag{4}$$

In the same manner we obtain,

$$Q_2 = \frac{q_{02}}{q_{01} + q_{02}} (1 - Q_0). \tag{5}$$

NEYMAN (1950) gave a method of evaluating these probabilities for a corresponding time-continuous process. A unit of time is divided into M intervals, each of duration $1/M$, and the transition probabilities are assumed proportional to the time lapse $1/M$; thus $q_{0i} = \lambda_i/M$. Time continuum is approached by letting $M \to \infty$, so that corresponding to P_{0i} we now have

$$P_{0i}{}^* = \lim_{M\to\infty} \left[1 - \left(1 - \frac{\lambda_i}{M}\right)^M\right] = 1 - e^{-\lambda_i} \tag{6}$$

Similarly, the Q_i are replaced by

$$\begin{aligned} Q_0{}^* &= e^{-(\lambda_1+\lambda_2)} \\ Q_1{}^* &= \frac{\lambda_1}{\lambda_1 + \lambda_2} (1 - Q_0{}^*) \\ Q_2{}^* &= \frac{\lambda_2}{\lambda_1 + \lambda_2} (1 - Q_0{}^*). \end{aligned} \tag{7}$$

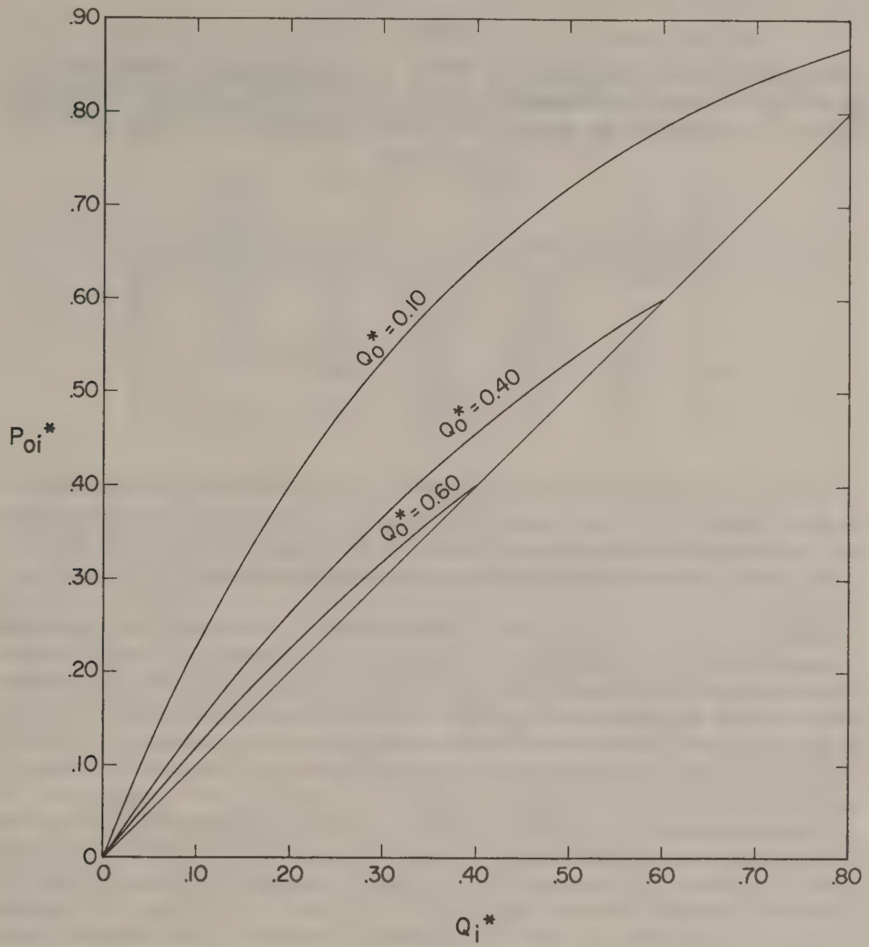

Figure 2. Relation between P_{0i}^* $(i = 1,2)$ and Q_i^* for various fixed values of Q_0^*.

Noting that

$$e^{-\lambda_i} = [e^{-(\lambda_1+\lambda_2)}]^{\frac{\lambda_i}{\lambda_1 + \lambda_2}} = Q_0^{*\frac{Q_i^*}{1 - Q_0^*}}, \tag{8}$$

we obtain the relation

$$P_{0i}^* = 1 - Q_0^{*\frac{Q_i^*}{1 - Q_0^*}}. \tag{9}$$

Given the Q_i^* we can obtain the P_{0i}^*. Figure 2 shows the relation between Q_i^* $(i = 1, 2)$ and P_{0i}^* for various fixed values of Q_0^*. The figure shows that P_{0i}^* is never less than Q_i^*, P_{0i}^* is strongly dependent on Q_0^*, and for any fixed Q_0^* the deviation of P_{0i}^* from Q_i^* is not constant, but reaches a maximum at an intermediate mixture of species 1 and species 2. Thus – according to the model – in a multiple-species fishery the CPUE as a density index for species i will tend to underestimate the "true" CPUE because of the presence

Table 1

Calculations showing adjustment of CPUE for multiple-species catch. Data are taken from Murphy and Shomura (1953). Each row represents the CPUE for a single day of fishing in the vicinity of Canton Island (lat. 3° S., long. 172° W.), July 1950

Catch/ 100 hooks yellowfin tuna	Total catch/ 100 hooks	$\hat{Q}_1$	$\hat{Q}_0$	$\hat{P}_{01}$	Catch/ 100 hooks yellowfin independent of other species	Increase in yellowfin CPUE
7·1	16·5	·071	·832	·076	7·6	0·5
3·2	7·8	·032	·922	·033	3·3	0·1
7·9	19·7	·079	·803	·084	8·4	0·5
1·3	2·7	·013	·973	·013	1·3	0·0
14·6	22·2	·146	·778	·159	15·9	1·3
0·0	3·9	·000	·961	–	–	0·0
13·2	17·8	·132	·822	·146	14·6	1·4

of species *j*, which competes with species *i* for space on the gear. The extent of underestimation is strongly related to the amount of empty space on the gear and to the apparent abundance of each species relative to the other. The tendency toward underestimation will be greatest in the years of highest apparent abundance.

In some fisheries – the Japanese longline fishery, for example – estimates of Q_0 may rarely be less than 0.90. Thus the underestimate of CPUE in these fisheries is likely to be small. The importance of a relatively small underestimate depends upon the manner in which the statistic is used. For example a seemingly small change in CPUE induced by correcting for a multiple-species catch might produce a large change in an estimate of total catch made from the relationship between total effort and CPUE.

The calculations for a specific example are given in Table 1. The data were obtained on cruise number 5 of the "Hugh M. Smith" in the vicinity of Canton Island (Murphy and Shomura, 1953). These particular data were selected for illustrative purposes because they had a wider range of Q_0's than that usually found for tuna longline data. The species of interest is the yellowfin tuna (*Thunnus albacares*); all the other species caught were pooled as species 2. The data reiterate the conclusion that the most severe underestimations occur at maximum CPUE's.

Estimation of Parameters

The probabilities, Q_i, that the hook remains empty, takes species 1, or 2, at the terminal instant of time are, under the previously stated independence assumption, parameters of the multinomial probability law. Mood and Graybill (1963; p. 238) derived the maximum-likelihood estimator for the mean of this distribution and the large sample variance of the estimator.

It may be noted, however, that the λ_i's are a more fundamental statistic than the P_{0i}^*'s since they can be computed for several components (year-classes, say) and then added to estimate a composite P_{0i}^*, whereas the P_{0i}^*'s themselves are not additive. When one works with components, the λ_i's can be reported as $-\log(1 - P_{0i}^*)$. It should be noted that the λ_i's have the properties of coefficients of instantaneous rates; for example, a λ_i of 1·0 represents an apparent abundance which is double that of a λ_i of 0·5. The maximum-likelihood estimator of the λ_i's is easily obtained from the n_i's by applying the invariant property of maximum-likelihood estimators to the Q_i^*'s,

$$\hat{\lambda}_i = \frac{n_i}{n_0 - N} \log \frac{n_{0\cdot}}{N} \tag{10}$$

If we make the reasonable assumption that large samples of the n_i's will have an approximately multivariate normal distribution, then the variances and covariance of the λ_i's are

$$\begin{aligned} \operatorname{Var}(\hat{\lambda}_i) &= \frac{1}{N}\left[\frac{\lambda_1\lambda_2}{1 - Q_0} + \frac{\lambda_i^2 Q_i^2}{\lambda_i^2 Q_0 - Q_i^2}\right], \\ \operatorname{Cov}(\hat{\lambda}_1, \hat{\lambda}_2) &= \frac{1}{N}\left[\frac{\lambda_1\lambda_2}{1 - Q_0}\right]. \end{aligned} \tag{11}$$

Estimates of Var ($\hat{\lambda}_i$) and Cov ($\hat{\lambda}_1$, $\hat{\lambda}_2$) are obtained by substituting the appropriate values of $\hat{\lambda}_i$ and $\hat{Q}_i$ into the above formulae.

Emphasis should be placed on the fact that the expressions in (11) are the *sampling* variances and the *sampling* covariance; they measure only the variation associated with repetitive sampling from a single population characterized by fixed λ_i's. These measures of variability must arise only from repetitive sampling since the model is constructed so that each λ_i is a constant and hence has zero variance. The constant λ_i's follow from the definition of the model where it is stated that the transition probabilities (the q_{ij}'s) are constant for all time intervals. In practice, samples may be drawn from several populations, each characterized by a different set of λ_i's. The resulting variance, in this situation, will be composed of at least two components: one owing to the variation among the several populations and the other owing to the chance variation which results from repetitive sampling from the same population. The expressions in (11) provide an estimate of the latter.

Discussion

Unfortunately, the analytic simplicity of a known number of hooks is not always available. In these circumstances it is possible to conjecture that the empty "space" of a gear is the complement of the maximum CPUE. This maximum is not, in general, a well-defined quantity. The maximum catch of a gill-net, for example, is a fish in every "hole". Although the attainment of this event is improbable, it is not impossible. Should the "saturated" or "supersaturated" condition (cf. Gulland, 1955) be used as a "maximum"? The concept of tolerance intervals (Dixon and Massey, 1957) may be helpful in establishing a lower bound on the maximum and, since the CPUE statistic is usually not easily treated parametrically, the table of distribution-free tolerance intervals given by Murphy (1948) will be of use.

Some problems of interpretation may also arise in evaluating the number of hooks actually fishing in the longline situation. Aside from the obvious problem of either the bait or the hooked fish falling off of the hook, the relation of hook depth to fish depth must be considered. The longline is comprised of units which hang in approximate catenaries from float lines. Each catenary contains several hooks which hang within a range of depths that may be as large as a few hundred metres. If the fish are excluded – by nature of their environmental tolerances – from some of the depths which the hooks occupy, then these hooks are in effect not fishing for the considered species. In the circumstance where hooks are recorded as actually fishing but are, in effect, not, Q_0 will be overestimated and the effect of competition (*i.e.* a value of P_{0i} for a particular value of Q_i) will tend to be underestimated.

It is important to note that adjustment of CPUE to account for multiple-species catches increases the variability of the adjusted CPUE's over the unadjusted ones. If environmental variables are important causes of fluctuation in abundance of any one species and these fluctuations tend to be minimized by multiple-species catches, then the environmental variables may be unrecognized or undetectable as causes of the fluctuations.

Finally, the competition model contains concepts that are applicable to other problems that arise in the study of harvested populations. These conceptual applications pertain to estimates of yield, estimates of survival rate, and optimum fishing strategies.

First, we note that natural and fishing mortality compete for the life of a fish just as species 1 and species 2 compete for a single hook. To express this competition we let S_0 denote the state where a fish escapes mortality; S_1, where the fish succumbs to fishing mortality; and S_2, where the fish succumbs to death from natural causes. Placing the problem in a more familiar notation, let $\lambda_1 = F$ (the coefficient of instantaneous fishing mortality) and $\lambda_2 = M$ (the coefficient of instantaneous natural mortality). Rewriting (7), gives

$$\frac{F}{F+M}(1 - e^{-(F+M)}), \tag{12}$$

which is the well-known expression for the fraction of a year-class taken by a fishery in a unit-interval of time (annual expectation of death from fishing). Multiplying (12) by recruitment provides an expression for yield, in numbers. Thus we have derived, using a probabilistic argument, an expression for yield that is identical to that which is conventionally derived deterministically. Furthermore, the assumption of an underlying multinomial-probability law enables estimates of the mean and variance of the λ_i's which are identical with F and M. Replacing F and M with their appropriate maximum-likelihood estimators from (10) gives a maximum-likelihood estimate of (12). The problem, here, of course, is to obtain data in terms of the number of fish that in some time interval are caught, succumb naturally, and remain alive. Perhaps tagging experiments are the most likely source of data of this type.

Second, survival rates are often estimated by means of a catch curve. Strong year-classes may arise and compete with other year-classes for space in the sampling gear. According to the model, the abundance of strong year-classes will be underestimated. Even under conditions of a stable age structure, several year-classes could compete with one another for space in the sampling gear. In a stable population the younger age-groups with the larger numbers of individuals would exert greater amounts of competition for becoming sampled than would older age-groups. It is conceivable that under some circumstances survival rate will tend to be underestimated as a result of competition among age-groups.

And, finally, the model suggests certain strategies for the fisherman. According to the model, the single-species CPUE resulting from fishing a fixed density of that species can be increased simply by setting the gear in a way or location such that the effect of competing species is reduced. The wisdom of this strategy is of course contingent on the monetary value of the competitor. Where the value of the competitor is often nil (*e.g.*, sharks in the Japanese high-seas longline fishery for tunas) it is to the fisherman's advantage to attempt to eliminate the competitor completely. On the other hand, the competing species may also be of value and the foregoing strategy would still increase the CPUE for the single species, but decrease the total CPUE. Thus, in a gradient of mixtures of two valuable species, the choice of fishing location would involve maximizing the monetary return from the combined catch.

Summary

The effect of multiple-species catches on the catch-per-unit-of-effort (CPUE) statistic for a single species is considered in terms of a simple stochastic model. The model enables computation for a single species of a CPUE which is independent of the effect of competition for space on the fishing gear by a competing species. According to the model, the adjusted single-species CPUE is never less than the multiple-species catch, the adjusted single-species CPUE is strongly dependent on the apparent abundances of the considered species, and the adjustment is not linear, but varies with the degree of species mixture. Various applications of the model are discussed and attention is called to the fact that the model provides a stochastic derivation of the well-known yield equation.

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ESTIMATES OF THE GROWTH OF SKIPJACK TUNA (*KATSUWONUS PELAMIS*) IN THE HAWAIIAN ISLANDS

by

B.J. Rothschild

ESTIMATES OF THE GROWTH OF SKIPJACK TUNA (*KATSUWONUS PELAMIS*) IN THE HAWAIIAN ISLANDS

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ABSTRACT

The von Bertalanffy growth parameters for skipjack tuna (*Katsuwonus pelamis*) were estimated from growth increments obtained during a tagging study conducted in the Hawaiian Islands in 1958. The estimate of K was 0.77 and L_∞ was 82.3 cm. These estimates were compared with skipjack growth estimates in the literature. The estimates given in the present paper must be viewed with caution since they are based on a relatively small sample, taken in a single year, in a single location.

INTRODUCTION

Growth of skipjack tuna (*Katsuwonus pelamis*) has been estimated from annulus interpretations, modal progressions in length-frequency distributions, and length increments of tagged fish. Each method has its shortcomings: It is difficult to detect valid year marks on hard structures; assumptions requisite for analysis of modal progressions are often uncertain; it is debatable to what degree relatively short-term recoveries, which are typical for tagged skipjack, actually reflect growth. Because of these uncertainties, it is not surprising that the published estimates of the growth of skipjack tuna disagree. This paper compares published estimates of growth with estimates derived from a tagging study in the Hawaiian Islands in 1958.

MATERIALS

The skipjack tuna were tagged near the islands of Oahu, Maui and Hawaii in May through September, 1958. Most of the fish were between 40 and 50 cm long when tagged. Several types of tags were used. To reduce possible variability, returns from only one are considered in this paper: the POFI-D2, lucite-headed dart tag. Both it and the method of its use are described in Yamashita and Waldron (1958).

Proc. Indo-Pacific Fish. Coun., 12(II): 100-111.

Since excessive handling of skipjack tuna can cause disproportionately high tagging mortalities (Marr, 1963) the tagged fish were not measured individually. Instead, fork length of the tagged fish was estimated by retaining and measuring a sample of fish from the school from which each tagged fish was obtained. This method is particularly practical for skipjack tuna, since they are likely to be of nearly uniform size in any school fished (Brock, 1954). The lengths of the tagged fish that were recovered were actual measurements.

The bias and precision of the estimated length at tagging were evaluated by comparing the measured length of each fish that was recovered after no more than 10 days at liberty with the estimated length at tagging for that fish. Under the assumption that growth during this short time at liberty was negligible, the length at tagging should exactly equal the length at recapture. Obviously this agreement will seldom happen, since estimation is involved. The assumption, however, permits the identification of size at recapture within 10 days as "length at tagging".

The estimated size at tagging is plotted with the "size at tagging" in Fig. 1. Recaptures for 10 or less days at liberty totaled 179 fish, but for clarity only representative points are plotted in the figure. If the measuring technique is, on the average, unbiased then a least squares fit to the data should provide a line which is identical to a 45-degree line passing through the origin. The least-squares line in Fig. 1 is

$$Y = 7.843 + 0.834 X$$

where Y is the estimated size of tagging, X is the "size at tagging".

We can see that the estimation procedure for these data, on the average, overestimates the size of fish less than 47 cm long, is unbiased for fish in the vicinity of 47 cm, and underestimates the size of fish more than 47 cm long. Since most of the fish were less than 47 cm long, the estimated size at tagging is generally overestimated and the increment of growth while at liberty is underestimated. The bias is small, however, exceeding 1 cm only at the largest and smallest lengths, and is therefore not considered a serious component of error.

It is also apparent from Fig. 1 that future tagging experiments with skipjack tuna should consider methods to increase the precision of the estimated length at tagging. This precision can be measured in terms of the deviations from the regression line in Fig. 1. The sum of squared of the deviations is 1,377 and the resulting standard deviation from regression is 2.8 cm. Thus, approximately 70 percent of the errors in estimated length at tagging are within ±2.8 cm and approximately 95 percent are within ±5.6 cm of the actual length at tagging.

The 1958 tagging yielded 708 returns. A preliminary examination of growth-increment data from these returns suggested that a considerably reduction in the variability of incremental growth relative to incremental growth could be obtained by considering only data from those fish recaptured after the longest time at liberty. A sample of reasonable size was therefore needed that contained fish that had been at liberty the longest. When the data were stratified by time at liberty, the stratum containing the fish that had spent the most time at liberty (171-420 days) consisted of 35 individuals. The data on each of these 35 fishes (Table I) were incorporated in this study of growth parameters.

TABLE I

DATA ON GROWTH OF SKIPJACK TUNA BASED ON 35 LONG-TERM RECAPTURES OF FISH TAGGED IN THE HAWAIIAN ISLANDS DURING 1958. THE ESTIMATED FORK LENGTH AT TAGGING HAS BEEN ADJUSTED ACCORDING TO THE FORMULA Y= 7.843 + 0.834X.

Estimated fork length at tagging (cm)	Measured fork length at recapture (cm)	Increment (cm)	Time at liberty (days)
45.7	58.7	12.9	171
96.8	53.1	6.4	174
46.7	60.6	14.0	175
42.3	52.0	9.1	178
42.3	51.6	8.7	178
45.2	56.3	11.0	180
46.3	52.2	5.9	181
44.6	57.0	12.2	182
42.9	61.0	17.6	187
45.2	58.0	12.7	187
50.1	63.3	13.8	191
53.0	56.6	4.6	195
93.5	62.5	18.6	198
45.2	58.0	12.7	199
49.6	50.5	8.2	201
46.3	64.7	18.4	201
44.6	54.5	9.7	204
37.4	53.0	14.3	226
40.8	58.9	17.3	226
53.3	66.2	13.9	252
59.2	64.5	7.2	252
45.2	60.3	15.0	256
45.7	60.1	14.3	259
45.7	61.1	15.3	260
46.3	62.6	16.3	308
45.2	61.4	16.1	312
46.3	67.2	20.9	319
46.3	62.4	16.1	321
45.2	62.6	17.3	323
44.5	66.0	21.3	324
44.5	65.0	20.3	335
45.2	64.0	18.7	358
46.3	66.9	20.6	377
46.8	68.4	21.7	378
44.5	70.5	25.8	420

ESTIMATION OF PARAMETERS

Fabens (1965) studied some of the properties of the von Bertalanffy growth function and provided a computer program to estimate, by an iterative least squares procedure, its parameters. I have assumed that t_o is equal to 0 and have employed the data in Table I in Fabens' estimation procedure to obtain values of 0.77 for K and 82.3 for l_∞.

DISCUSSION

Other studies on the growth of skipjack tuna have been performed on fish from Japanese waters (Aikawa and Kato, 1938; Kawasaki, 1955a, 1955b), the central Pacific (Brock, 1954) and the eastern Pacific (Schaefer, Chatwin and Broadhead, 1961). A concise statement of the results of these studies may be found in Waldron (1963) and Bell (1964). Kawasaki (1963) published a recent paper on growth of skipjack.

The estimates by Aikawa and Kato were based on an interpretation of rings on the vertebral centra. Their estimates indicate a considerably smaller size-at-age and a much higher attainable age than any of the growth estimates made for fish of the eastern and central Pacific. Either skipjack in Japanese waters grow at a substantially slower rate than those studied in other parts of the Pacific or Aikawa and Kato's estimates are in error. The latter possibility is suggested by the fact that their growth curve is essentially a straight line over a rather long span of age; furthermore, no serious attempt was made to validate the annuli as year marks.

Kawasaki (1955a, 1955b) apparently used the ages assigned by the early Japanese workers but his estimates of growth (see Kawasaki, 1963) based on an analysis of modal groups were slightly less than those computed in this paper (Fig. 2).

Schaefer et al. (1961) gave growth estimates on tagged fish in terms of a regression (Y = a + bX) and a regression through the origin (Y = bX) of growth on days at liberty. They gave in the regression example annual increments of 173, 106 and 58 mm for skipjack 400-499, 500-599 and larger than 600 mm, respective. For a regression through the origin they gave 207, 116 and 1 mm for fish 400-499, 500-599 and larger than 600 mm, respectively. A general average was computed at 124 mm per year for the regression and 122 mm per year for the regression through the origin. The tagging studies of Schaefer et al. show growth which is perhaps slightly less than that estimated in this study (Fig. 3).

Schaefer et al. (1961) have concluded that their estimates of growth from tagging are significantly less than estimates of growth from modal progressions of skipjack taken in the eastern Pacific. This conclusion may not have been warranted. If their yearly increments are considered on a size-specific basis (e.g., the increment for the 400-499 mm group rather than the general average) it is seen that the growth inferred from tag returns closely approximates the growth estimated by modal comparing Fig. 3 and Fig. 4; the increments of 173 and 207 mm given by Schaefer et al. approximate both the VBGF from the Hawaiian data and the growth envelopes from modal-progression data of the eastern Pacific fish.

Brock (1954) estimated a greater rate of growth than that given in this and the other papers (Fig. 5). His estimate was based on modal progressions of length-frequency samples of skipjack from Hawaiian waters. Brock's estimate of the growth rate of skipjack tuna may be too high or possibly all of the other curves underestimate growth rate.

Brock's method, in essence, designates the smallest summer modal group as 1-year-old fish and the next largest summer modal group as 2-year-olds. Although the mode for his "1-year-old" fish well may be fairly accurate, it is possible that the modal length of 2-year-old fish is overestimated. This error could result if his "2-year-old" group is based on an overlapping "poly-age" distribution. As the average age of this poly-age modal group increases, its average size also would increase; the apparent age would, however, not change; an overestimate of growth must result. Secondly, according to hypotheses suggested by Rothschild (1965) skipjack tuna maintain a size-specific movement pattern between the eastern and central Pacific Ocean. It is likely, as a part of this pattern, that fish approximately 2 years old have not completely entered the central Pacific. Thus it is possible that "2-year-old" fish are not fully recruited in the central Pacific skipjack fishery. Less than full representation of the "2-year-old group" in Brock's poly-age modal group could accentuate a possible overestimation.

On the other hand, there are two reasons why the curve estimated in the present paper may underestimate actual growth; tagging may have reduced growth or size-specific movements may have caused an undersampling of the faster-growing fish, which might not remain in the fishery as long as the slower-growing ones. As previously pointed out, no evidence exists now to substantiate the assumption that tagging affects skipjack growth. Size-specific movements do, however, seem to operate, since the month-to-month increments in modal lengths of skipjack (Rothschild, 1965) do not appear to represent growth, but remain nearly constant throughout the year. The effect of size-specific movements on the estimation of growth from the tagged fish depends on the extent to which the tagged fish which have been recaptured either grow as does the bulk of the population, but exhibit a typical movement, or the extent to which the recovered fish grow more slowly than the bulk of the population and for this reason are more susceptible to capture because of their longer stay in the fishery; it is difficult to decide which alternative is applicable.

The risks of basing a generalization of growth on 35 tag returns in a single year are clearly recognized. Also evident is the likelihood that skipjack tuna from the eastern and central Pacific comprise subpopulations distinct from skipjack taken in Japanese waters. These considerations suggest not only that possible growth differences among years might influence comparisons, but also that growth might differ among locations. The extent to which the curve derived in this paper agrees with most of those in the literature, and the difficulty and expense of obtaining this sort of data on tunas in general, make it reasonable to retain the estimates given here as an approximation for further studies on the population dynamics of the skipjack tuna.

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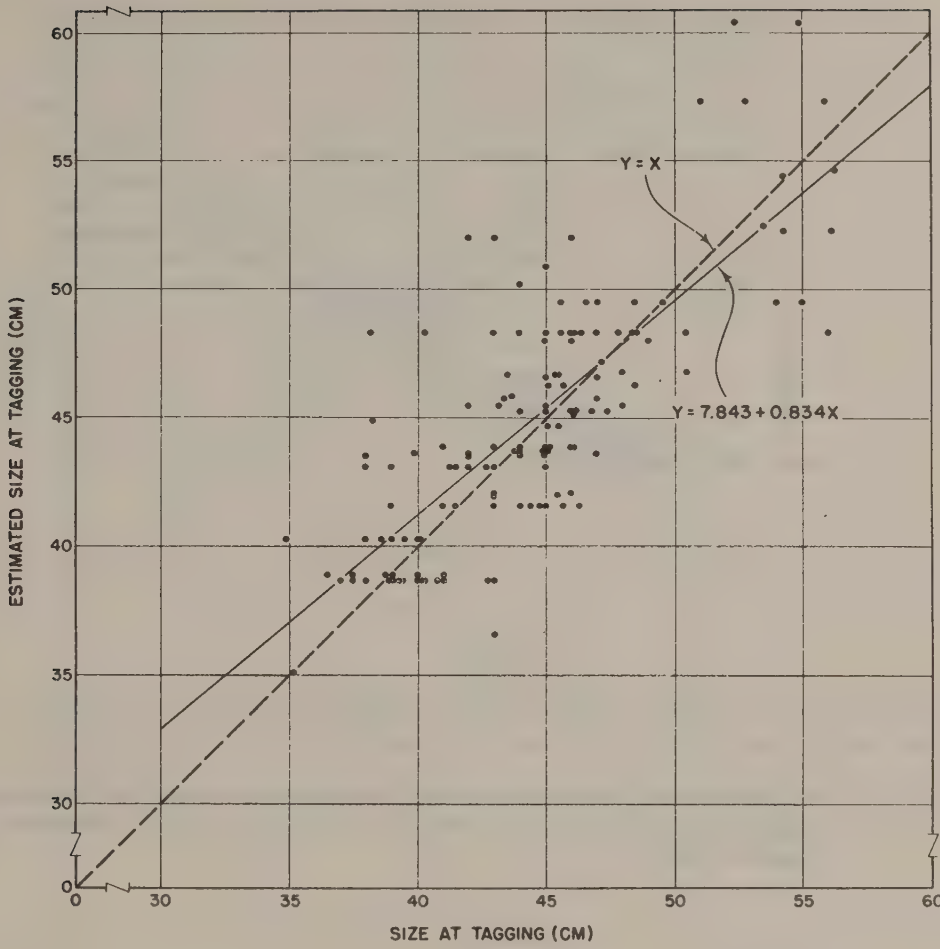

Fig. 1. Regression of Estimated Size at Tagging on "Size at Tagging" Determined from Recaptures within 10 Days for Skipjack Tuna Tagged in Hawaiian Waters. For Clarity Only Representative Points are Plotted

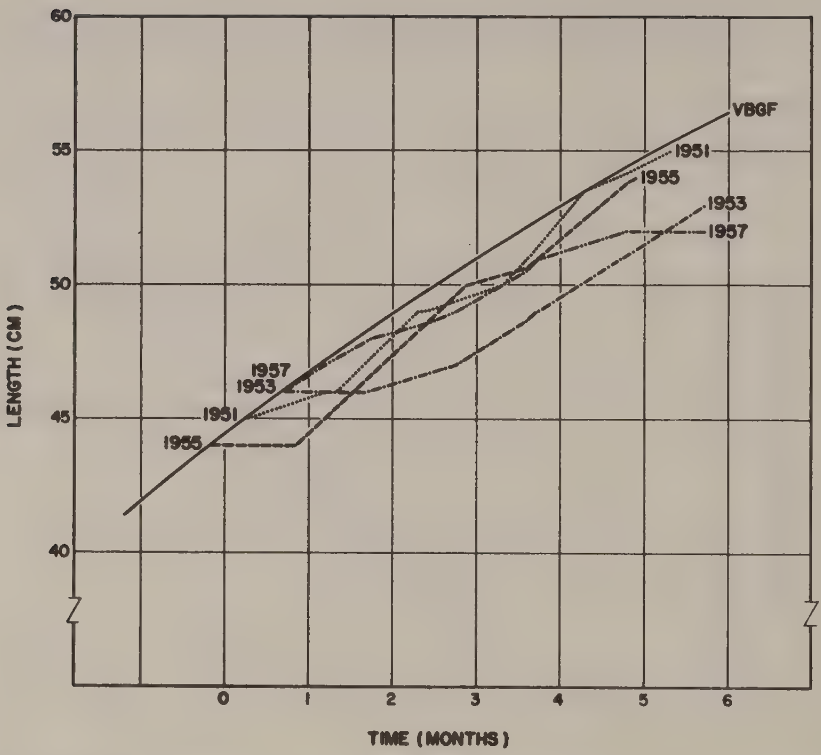

Fig. 2. Size-Specific Comparison of Skipjack Growth Curves for Selected Years from Kawasaki (1963) with the VBGF (L_∞ = 82.3, K = 0.77) Estimated from Hawaiian Tagging Data

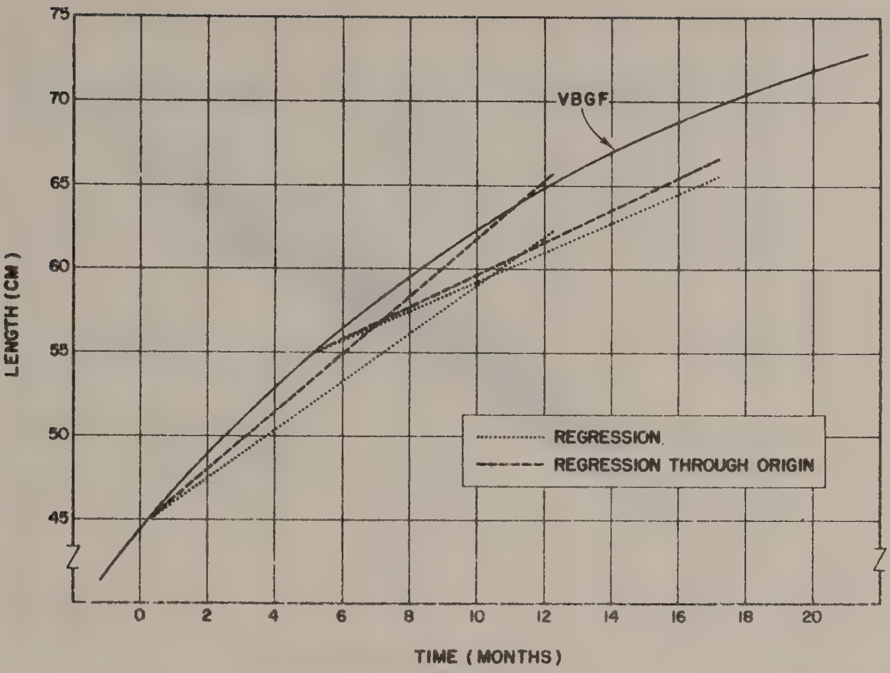

Fig. 3. Comparison of Skipjack Growth Estimated in the Eastern Pacific Ocean from Tag Returns (Schaefer et al., 1961) and the VBGF Estimated from Tag Returns in Hawaii

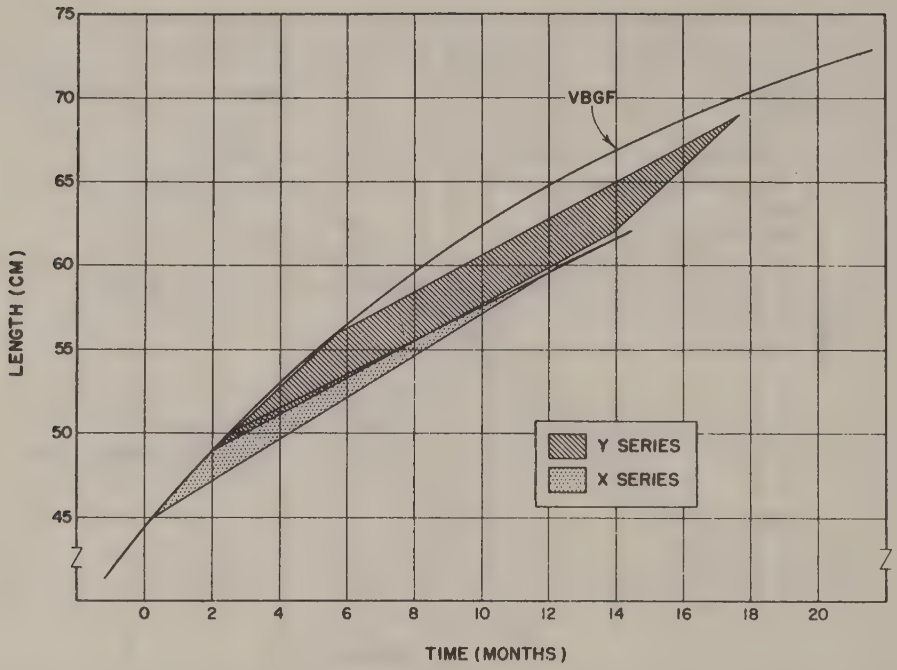

Fig. 4. Comparison of Skipjack Growth as Estimated from Modal Progressions in Length-Frequency Distributions of Eastern Pacific Ocean Samples (Schaefer, 1961), and the VBGF Estimated from Tag Returns in Hawaii. The Modal Progression Estimates are Given Here as Envelopes of Points

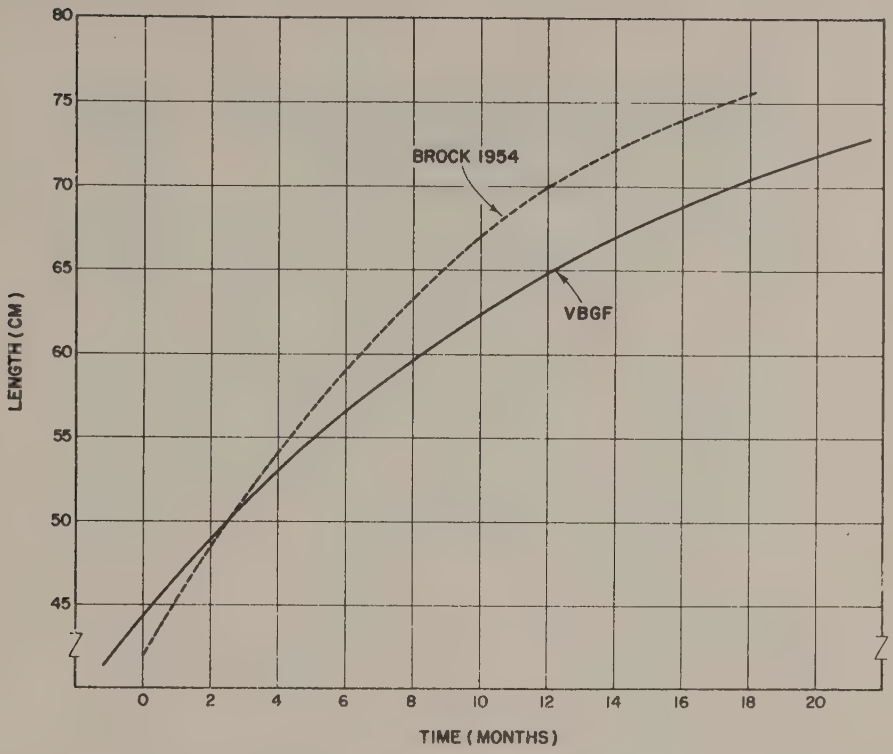

Fig. 5. Comparison of Brock's (1954) Estimate of Skipjack Growth with the VBGF Derived from Tag Returns in this Paper

Dentition of Newborn Steller Sea Lion, Eumetopias jubatus **(Schreber, 1776)**

By Victor B. Scheffer, Seattle

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Dentition of Newborn Steller Sea Lion, Eumetopias jubatus **(Schreber, 1776)**

By Victor B. Scheffer, Seattle

With 2 Figures

Received 1. III. 1966

Twenty years ago I examined four newborn sea lions and reported that five or six teeth in each quadrant had gingivally erupted (Scheffer, 1945, p. 392). I did not then distinguish between deciduous and permanent teeth. I have recently examined three other specimens (Table 1) and find that the dentition is mixed.

Table 1: Specimen data for late fetal and newborn Steller sea lions from Alaska

Specimen number	Age	Sex	Date	Length cm.	Weight kg.	Condylobasal length mm.
U.S. – 60–3702 1)	late fetus	♀	21 May 1960	100	20.0	164
26–6–65 B 2)	1 wk.?	♀	26 June 1965	96	18.6	177
26–6–65 A	2 wks.?	♂	26 June 1965	93	17.9	177

1) Cleaned skull only. Photographs of the jaws of the other two specimens were taken in the flesh.
2) With frayed umbilicus 4 cm. long (Fig. 2).

On the basis of the recent specimens, and allowing for the fact that two of them are not strictly "newborn" but are 1 or 2 weeks old, the count of gingivally erupted teeth at birth is approximately:

$$\frac{I1 - I2 - i3}{I2 - i3}\ \frac{c}{c}\ \frac{p2 - p3 - p4}{p2 - p3 - p4} = 13$$

In this formula, small letters indicate deciduous teeth and large letters permanent teeth are spicules only 1 or 2 mm long.) Although 28 permanent teeth are unerupted incisor in locus 1 is absent in all pinnipeds. The dentition of individual sea lions undoubtedly varies from the formula given, for in the specimens at hand the crown tips of certain unerupted permanent teeth are near the surface, and certain of the deciduous incisors are about to be shed.

Eumetopias has no second upper molar. This tooth is represented in all other genera of otariids, though it may be absent in individuals. I examined the dentitions of 10 adult ♂♂ and 10 adult ♀♀ Steller sea lions from Alaska in the collection of Fiscus (1961, Table 2) [1]). In none is there an upper M 2. The maxilla of *Eumetopias* has a large diastema between the premolar series and the molar. The molar is situated far to the posterior. There is evidently no room for a second molar. The diastema is barely noticeable in the newborn pup (Fig. 1 & 2); it widens to about 4 cm in the old ♂.

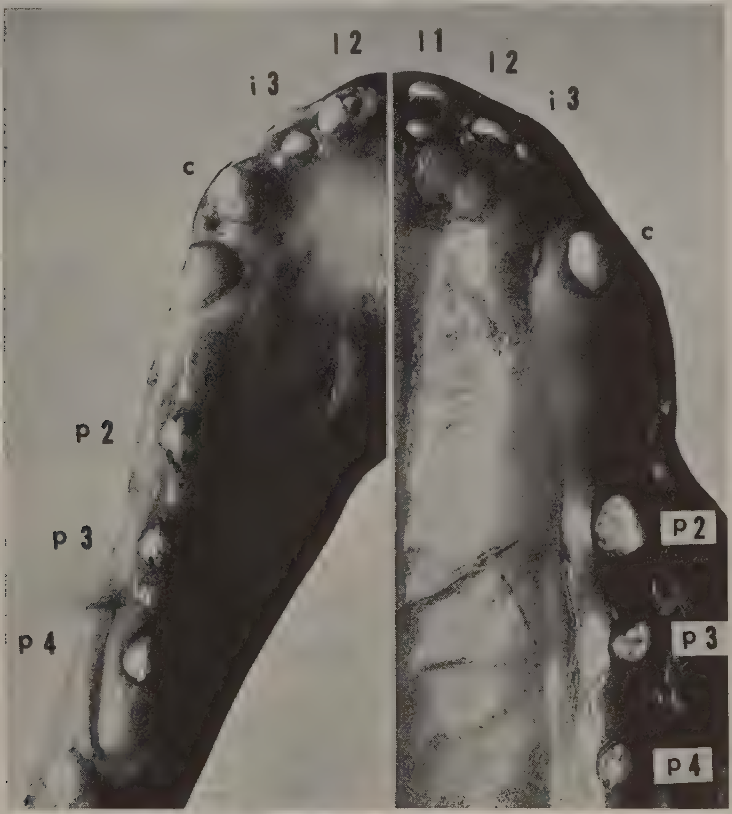

Fig. 1: Left upper and lower jaws of *Eumetopias jubatus*-♀ estimated age 1 week, Walrus Island, Alaska, 26 June 1965. (Small letters indicate decidous teeth and large letters permanent teeth. Natural size.)

The specimens exhibit the complete deciduous-plus-permanent dentitions of *Eumetopias,* or 60 teeth, with the following exceptions: they have no deciduous median incisors (upper i 1 and i 2, and lower i 1). Valid assumptions are that these teeth are vestigial, that they remain hidden in the gums, and that they are usually lost when skulls are cleaned by dermestid beetles. (In the fur seal, *Callorhinus*, the corresponding teeth are spicules only 1 or 2 mm long.) Although 28 permanent teeth are unerupted in the sea lion at time of birth, all are well formed. Superficially, at least, their crowns appear to be complete.

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[1]) A misprint appears in Table 3 of the paper by FISCUS; M 2 and M 4 should read P 2 and P 4.

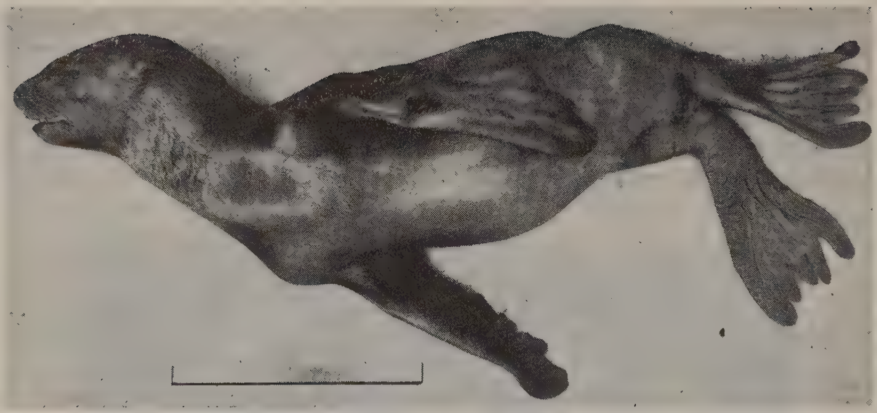

Fig. 2: *Eumetopias jubatus*-♀ estimated age 1 week, Walrus Island, Alaska, 26 June 1965. (30 cm ruler.)

The Steller sea lion pup has about 26 erupted teeth and the fur seal pup has about 38 (Scheffer & Kraus, 1964, Fig. 5). The relative delay in transition from deciduous to permanent teeth in the sea lion pup suggests that the weaning date is also delayed. (As this paper goes to press, I find that Spalding (1966) has already come to the same conclusion.) The fur seal pup is weaned in early November at age 4 months (Peterson, 1965, p. 155). In both species the anterior permanent teeth develop earlier than the posterior ones-probably an adaptation for sucking.

Table 2: Mixed dentitions of late fetal and newborn Steller sea lions 1)

Locus		Status of gingival eruption	
		Deciduous teeth	Permanent teeth
Upper jaw			
Incisor	1	?	+
,,	2	?	+
,,	3	+	—
Canine	1	+	—
Premolar	1	0	—
,,	2	+	—
,,	3	+	—
,,	4	+	—
Molar	1	0	—
Lower jaw			
Incisor	1	0	0
,,	2	?	+
,,	3	+	—
Canine	1	+	—
Premolar	1	0	— 2)
,,	2	+	—
,,	3	+	—
,,	4	+	—
Molar	1	0	—
Total no. teeth erupted		10	3 or 4

Symbols: + = erupted; — = not erupted, 0 = no tooth in this locus in pinnipeds, ? = status uncertain (see text).

1) Based on three specimens with similar dentitions (Table 1). — 2) Lower P 1 has just erupted in specimen 26–6–65 A.

Summary

The Steller sea lion has 60 teeth: 28 deciduous and 32 permanent. In the newborn pup about 26 teeth have erupted from the gum (20 deciduous and 6 permanent). 6 anterior incisors are unaccounted for and are presumed to be vestigial; 28 teeth are permanent, well formed but; yet unerupted.

Zusammenfassung

Das Gebiß des neugeborenen Stellerseelöwen, *Eumetopias jubatus* (Schreber, 1776)

Der Stellerseelöwe *(Eumetopias jubatus)* hat 60 Zähne: 28 Milch- und 32 Dauerzähne. Beim Neugeborenen sind bereits 26 Zähne (20 Milch- und 6 Dauerzähne) durchgebrochen. 6 vorangehende verkümmerte Schneidezähne rechnen nicht dazu. 28 weit vorgebildete, noch nicht durchgebrochene Zähne sind Dauerzähne.

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15 CENTS – 67-8

THE KILLER WHALE

by Victor B. Scheffer

Mention *killer whale* in the Pacific Northwest and you are in an argument. "Vicious – bloodthirsty – eats its own weight of salmon in a day." But "magnificent – unique – harmless – an asset to the Northwest."

Public interest in the killer whale *(Orcinus orca)* was stimulated by the capture of Moby Doll in 1964 for the Vancouver Public Aquarium and Namu in 1965 for a privately owned Seattle aquarium.

The killer whale cruises in all months of the year through waters of the Northwest. It ranges, in fact, through all seas of the world, to the very limits of polar fast-ice. No one knows its numbers, though for the State of Washington several hundred would probably be a closer guess than several thousand.

In the North Pacific Ocean the male attains a known length of 27.2 feet and an estimated weight of 9 tons, the female a known length of 22.9 feet and a known weight of 7.9 tons. (Lengths up to 31 feet for males and 27 for females have been reported by Japanese whalemen.) The newborn calf is about eight feet long and weighs an estimated 1,000 pounds. The large triangular dorsal fin of the male attains a height of 5.6 feet, that of the female about three feet.

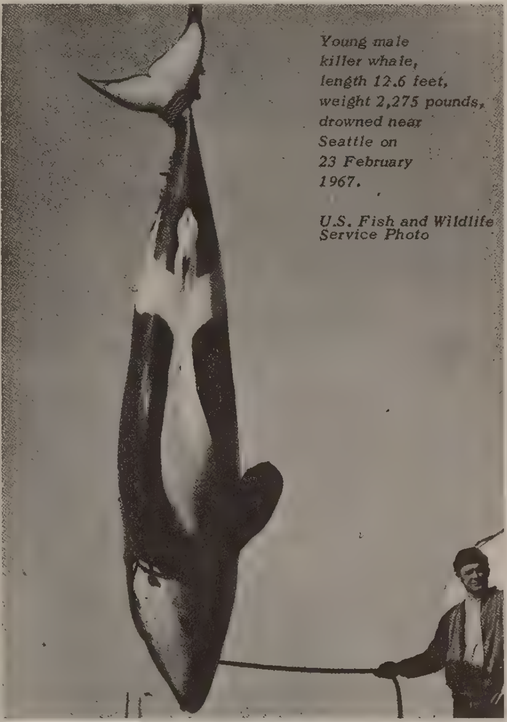
The flipper or "hand" is broad and rounded, like a ping-pong paddle. In the male it may reach a length of 6.7 feet and a width of four feet. The width of the tail flukes, tip to tip, in a large male is nine feet.

The color pattern of the adult is striking black and white with some gray. The white areas on the adult are yellowish or light yellowish brown on the newborn. All-white individuals (albinos) have often been seen around Vancouver Island.

Little is known of the breeding habits of the killer whale. From the evidence of the varying stages of development of fetuses in females taken commercially by Japanese and Soviet whalers mating may be year-round. Nothing is known of the gestation period, though by analogy with another large delphinid (the pilot whale), it may be 13 to 16 months. Only one calf is produced at a time. The two mammary teats are hidden in slits on the streamlined body far back of the navel. The killer whale is probably polygamous.

The penis is completely retractile and, on a 22-foot male, measured 3.5 feet long. A chance aerial photo by S. Takashima on June 22, 1957, showed two killers in copulation near the surface of the sea, belly-to-belly.

The killer whale is highly social, habitually traveling in packs of two to 40 individuals. "Family togetherness" is a way of life. Females and young are said to stay slightly apart from the bachelors and bulls. Locally, the social instinct of the killer whale has been exploited for the purpose of capture by firing a 16-inch harpoon into the back of the largest male, presumably the group leader or "pod bull". A brightly-colored float trailing from the harpoon allows the hunter to follow the group for days or weeks.



Young male killer whale, length 12.6 feet, weight 2,275 pounds, drowned near Seattle on 23 February 1967.

U.S. Fish and Wildlife Service Photo

Ian MacAskie writes that he was on one of three small patrol vessels in British Columbia in 1964, drifting quietly. Suddenly the vessels started their engines simultaneously. Five killer whales popped to the surface – heads up, close ranked, poised for a second like dancers in a ballet.

Dave and Melba Caldwell, of Los Angeles County Museum, have summarized care-giving behavior in killer whales. A mortally wounded mother stood by her dead calf, circling the body for an hour until she died, though she never attacked the collector's boat. Another female lingered three days near Hat Island, Puget Sound, after her calf was killed. A crew from Marineland of the Pacific captured a large female near Bellingham, but the lasso caught in the ship's propeller. "As she struggled in the water, she emitted a high-pitched, penetrating vocalization. After twenty minutes the high dorsal fin of a male killer whale appeared and the animal 'zeroed in on the female as if by radar' . . . . The two animals together charged toward the boat at high speed, veering only when they had approached to within five to eight feet . . . then together charged again. This time they struck the boat." The crew killed both whales to save the boat.

The ability of some cetaceans to talk underwater was first proved in the mid-1950's. The Royal Canadian Navy first recorded killer whale sounds under water among the Queen Charlotte Islands in 1956. W. E. Schevill and W. A. Watkins, who studied the voice of Moby Doll, reported that all the sounds are *clicks*. When fast-repeated, the clicks resemble a *scream*. The strident screams are apparently used for communication – calling – and the separate clicks for echolocation. Some zoologists believe that failure of echolocation may cause killer whales to run aground in shallow water. Among the many stranding records is the mass death of twenty killers on a New Zealand beach in 1955. Sympathetic onlookers at the disaster tried to save a few whales by heading them out to sea, but the whales turned back and died with their fellows.

Little is known about the causes of death among killer whales. The first killer ever taken alive died 18 hours later; she had an acutely inflamed intestine, pneumonia, an old fracture of the lower jaw and excessive tooth wear. The maximum life span of the killer is at least 25 years, as indicated by growth rings on the roots of the teeth.

Is the killer whale a peril to man? Roger Caras, in his 1964 book *DANGEROUS TO MAN*, says that "*there has not been one single authenticated attack.*"

The story of H. G. Ponting, photographer for the Scott party to the South Pole in 1911, has often been told. He was standing on Ross Sea ice and training his camera on a group of killer whales. "I had got to within six feet of the edge of the ice – which was about a yard thick – when, to my consternation, it suddenly heaved up under my feet and split into fragments around me; whilst the eight whales, lined up side by side and almost touching each other, burst from under the ice and 'spouted'." Did the killers take him for a seal? We will never know.

The name "killer" originated, of course, from the whale's habit of taking warm-blooded prey. His enthusiasm for the job of satisfying his appetite comes from a survival instinct similar to that of a hungry wolf in a herd of sheep; it is often mistaken for a so-called joy of killing. The killer is the largest and swiftest of the marine mammals that eat warm-blooded prey. Its top speed is about 30 land-miles per hour. J. H. Prescott saw a male killer leap clear of the water holding an adult sea lion crosswise in his jaws! The teeth are stout, deeply rooted and concial, numbering about 46 to 50 in the adult. Evidently they take quite a beating, for in old whales they are often worn to the gum-line, or even to a depth where the pulp cavity is exposed and infection sets in.

How often the killer whale feeds is unknown. Moby Doll (actually a male) fasted 54 days before he took food; then he ate 100 to 200 pounds of fish daily, or 4 to 8 percent of his body weight, until he died a month later. In captivity he was offered a choice of food and took in order of preference: salmon, lingcod, Pacific cod, certain rockfishes, ratfish (after the spines had been removed) and other fishes.

Japanese whaling captains from 1948 to 1957 recorded the contents of 364 killer whale stomachs with food. The remains were, in order of occurrence: fishes (cod, flatfishes, sardine, salmons, tunas, and other); squids and octopuses; dolphins (Dall and True, blue-white, and finless black); whales (beaked, sei, and pilot); and seals (harbor and ringed). Salmons were in 1.6 percent of the stomachs. Soviet biologist Ivanova found "fish and squid" but no sea mammals in 10 stomachs from the Kuril Islands.

The main food items, fishes and squids, are not the ones which fill our literature with accounts of "savage" attacks upon sea birds, seals, sea otters, porpoises, and whales. Killer whales undoubtedly attack their marine associates very efficiently. The evidence comes from stomach examinations, from eye-witness stories, and from observations of the parallel scars, spaced like killer whale teeth, on the backs of seals and whales. The bloodiest stories tend to be untrue or distorted.

D. F. Eschricht is said to have found remains of 13 common porpoises and 14 seals in *one* killer whale stomach, but when we turn to the original 1862 account we find that the remains were fragments of skin and bones representing animals eaten over an unknown period of time. Charles Bryant is supposed to have pulled 18 and 24 Alaska fur seal pups from the stomachs of two killers, though the story actually originated among the harp-seal fishermen of the North Atlantic and was probably embellished in the re-telling.

Though the killer whale has great recreational appeal, it has no commercial value in the United States. In Asian waters it is hunted for its fine, clear oil, its fresh meat for human food, and its scrap meat for fertilizer and fish bait.

Is the chasing of killer whales in our local waters legal? ethical? humane? Since 1965, six whales have admittedly been killed by Seattle showmen; many others have been quietly killed or mortally wounded by harpoons, drug-syringes, and nets. All were *legally* destroyed. No laws of any kind protect the smaller cetaceans of North America. Should individuals have the right to harass and maim wild animals which belong to all residents of the Pacific Northwest? The highly integrated social behavior and intelligence of this mammal will allow him to learn through experience, sensitized by the bloodshed of his fellows, to avoid areas of known danger. Must we all lose the thrill of seeing these magnificent beasts free, unalarmed and approachable because individuals seek profit or fame?

I suggest (first) that marine mammals for exhibition be captured in regions remote from population centers. I suggest (second) that those marine mammals not now protected by law in Washington, including the smaller cetaceans, the harbor seal, and the sea lion, be classed as "game" animals and thus be drawn into a wildlife management plan. This change would not be equivalent to classing them as "sport animals." The State Game Department is the only agency with legal authority to regulate the hunting of such animals. A game-permit system would insure that some responsible official would be present during the chasing and handling of whales – those operations which up to now have been well hidden under a smoke screen of trade secrecy. Responsible supervision would extend to the care of the mammals after capture, with attention to clean water and living space.

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19. *Marine Mammals and the History of Bering Strait*

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We deal here with the question: "Do differences between the marine mammal faunas of Pacific and Atlantic sectors of the Arctic-Subarctic provide evidence of interchange via Bering Strait during the late Cenozoic?" The differences to be discussed are geographical and morphological. It is well to caution that taxonomic arrangements currently expressing these differences are still provisional. For example, of the 27 genera mentioned, 19 are monospecific. To a land-mammal taxonomist, this ratio of genera to species will seem high. How truly the ratio represents the phylogeny of the marine mammal groups is by no means clear.

The "Arctic" is defined broadly as the region where marine mammals are regularly associated with permanent ice, the "Subarctic" with temporary ice. The words "race" and "subspecies" are used interchangeably.

Writers who have speculated on population spread and speciation among northern marine mammals include Davies, King, McLaren, Simpson, and Udvardy (see references). I have been helped by studying their conclusions, and especially by discussing them with V. Standish Mallory.

General Features of Marine Mammals

Recent marine mammals include most of the Cetacea, the Sirenia, and the Pinnipedia (all three orders also have freshwater representatives), and one of the Carnivora, the sea otter. All have flippers—flattened digits—on at least one pair of limbs. They gather submarine food and cache no part of it for future use. They give birth in the open to single, large, precocious young, and they do not use nest materials. No other mammal has all of the preceding characteristics.

Scheffer and Rice (1963) recognized 116 species of recent marine mam-

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mals. We shall review 16 of these in some detail, concentrating especially on those that regularly enter the Bering-Chukchi region or could have entered it during late Cenozoic time. Other species are mentioned briefly, including those that live in temperate waters south of, and adjacent to, the Subarctic.

At least four marine-mammal traits have implications for the spread of populations and the splitting of races.

First, many cetaceans and some pinnipeds are migratory, feeding in one place and breeding in another (Clarke, 1957). The migratory route of the northern fur seal is about 5,000 km each way, and of the California gray whale about 5,500 km. Migration is a curious trait; some mammals have adopted it and others have not: the fur seal moves north in summer to breed; the gray whale moves south in winter to breed; the sea otter breeds in any month without leaving its home waters. In the evolution of the migratory habit, the seasonal exodus to food-rich waters has probably been a more important factor than seasonal return to suitable breeding grounds. When temperatures dropped and seasons became more pronounced in the late Miocene and early Pliocene (Wolfe and Leopold, this volume), food organisms such as plankton, fish, and squid in the marine pastures of the north must have changed both quantitatively and qualitatively. Coincident with these changes, the seasonal movements of certain marine mammals may have begun. Today, migration routes are deeply engraved in the behavior patterns of many marine mammals.

Second, individuals may stray far from home. An Alaskan(?) ribbon seal was captured in Morro Bay, California, as were a Mexican(?) elephant seal in southeastern Alaska, an Atlantic harp seal and a Pacific fur seal near the mouth of the Mackenzie River, and ice-dependent hooded seals in Portugal and Florida. As a result of wandering, new colonies have become established.

Third, all pinnipeds are able to travel on land and ice. In this respect they differ from cetaceans; they are free to cross a barrier into new waters. Mummified crabeater seals have been found 30 miles from Ross Sea and up to 3,000 feet above sea level in Antarctica. Walruses may travel 15 to 20 miles overland in an emergency.

Fourth, many cetaceans and pinnipeds are "antitropical" (Davies, 1963). They shun warm water. Though the ancestors of certain species are presumed to have crossed the equator in cooler epochs (post-Miocene), the modern species now hold to higher latitudes. According to Davies (1960), antitropical representatives of the pilot whale *Globicephala melaena* are approaching subspecific distinction after separation near the end of the last ice age, about 11,000 years ago.

Arctic and Subarctic Marine Mammal Faunas

Sixteen species of northern marine mammals are listed in Table 1. The list is based largely on distributional records from the following sources: marine mammals, Scheffer and Rice (1963); cetaceans, Nasu (1963), Sergeant (1961), Slijper (1962), and Tomilin (1962); pinnipeds, King (1964) and Scheffer (1958). Fossil records are largely from King (1964), Lepiksaar (1964), Matthes (1962), and Simpson (1945).

Each number in the right-hand column of Table 1 refers to a species discussed below.

CETACEA; ODONTOCETI

1. The killer whale *Orcinus orca* is monotypic, cosmopolitan, and temperature-tolerant. It ranges north to Novaya Zemlya, Svalbard, Greenland, Baffin Bay, Chukotka Peninsula, and Alaska. It is believed to range widely through the Arctic Ocean; certainly in Antarctica it penetrates to permanent ice.

2. The harbor porpoise *Phocoena phocoena* inhabits coastal waters of the North Atlantic and North Pacific, north to the Arctic Ocean in summer.

TABLE 1. *Comparison of Recent Marine Mammal Faunas of Pacific and Atlantic Sectors of the Arctic and Subarctic*[1]

Species	Earliest Known Fossil Occurrence of Genus	Levels at Which Pacific and Atlantic Forms Differ	Rank
ARCTIC REGION			
Delphinapterus leucas	Pleistocene	Subspecific	3
Monodon monoceros	Pleistocene		4
Balaena mysticetus	Pliocene		8
Pusa hispida	Pliocene	Subspecific	10
Histriophoca fasciata	Pleistocene	Generic (i.e., in Pacific only)	12
Pagophilus groenlandicus	Pleistocene	Generic (i.e., in Atlantic only)	13
Erignathus barbatus	Pleistocene	Subspecific	14
Cystophora cristata	Pleistocene	Generic (i.e., in Atlantic only)	15
Odobenus rosmarus	Pleistocene	Subspecific	16
SUBARCTIC REGION			
Orcinus orca	Pliocene		1
Phocoena phocoena	Pleistocene		2
Balaenoptera physalus	Pliocene		5
Balaenoptera acutorostrata	Pliocene		6
Eschrichtius gibbosus	Pleistocene	Subspecific (?)	7
Phoca vitulina	Miocene	Subspecific	9
Halichoerus grypus	Pleistocene	Generic (i.e., in Atlantic only)	11

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[1] The species are ranked in the right-hand column roughly in order of phyletic age and specialization for marine life; those first are thought to be the most remote from terrestrial ancestors.

Circumboreal communication since the last glaciation has presumably allowed some intermingling of Pacific and Atlantic stocks, for members of the two are indistinguishable.

3. The beluga *Delphinapterus leucas* ranges around the rim of the Arctic Ocean and regularly into cold waters of adjacent seas (Kleinenberg *et al.*, 1964, p. 257). At least three subspecies are recognized—from the White Sea, Arctic, and Far-Eastern Seas of Siberia—though Sergeant (1962, p. 2) stated that there are "probably many local stocks or races." In the waters between Alaska and Siberia, the beluga moves regularly as far south as northern Bering and Okhotsk Seas, and occasionally to Sakhalin. With the coming of each glaciation, the beluga was presumably able to find refuge as isolated populations in marine, brackish periglacial, or estuarine waters along a shoreline that then lay at the outer edge of the continental shelf.

4. The narwhal *Monodon monoceros* is nearly confined to the Arctic Ocean; it is the most polar of all cetaceans and is monotypic. It is more abundant on the Atlantic than on the Pacific side. In Bering Sea, tusks have been found as far south as St. Lawrence Island. Narwhals move about through channels in ice along the shore, sometimes in large groups. During glacial stages they would have taken refuge in broken ice of the North Atlantic. They would have been pushed south not only by fast ice but also by lowering of sea levels and seaward migration of shorelines.

CETACEA; MYSTICETI

5. The finback whale *Balaenoptera physalus* is cosmopolitan. It moves north in spring in the western Bering Sea and penetrates far into the summer ice of Chukchi Sea. It is the most abundant Pacific subarctic whale. Finbacks from the North Pacific and North Atlantic are indistinguishable.

6. The little piked whale *Balaenoptera acutorostrata* is cosmopolitan. It penetrates to Arctic ice fronts in summer and is believed to go farther into polar ice than any other rorqual. It tends to be coastal, strongly migratory, often solitary. Little is known of its movements in the North Pacific and adjacent seas (Norris and Prescott, 1961; Fiscus and Niggol, 1965), though its habits have been studied near Norway. Little piked whales from the North Pacific and North Atlantic are indistinguishable.

7. The gray whale *Eschrichtius gibbosus* is represented by two populations—Californian and Korean. A third (North Atlantic) population, now extinct, may have persisted into historic time; it is known from subfossil remains from Sweden, England, and Holland. It "must have occurred still along the European coasts in the first centuries A.D. Along the American coast of the Atlantic this species still must have been present in the begin-

ning of the 18th century, for at that time it was still caught by the whalers" (Van Deinse and Junge, 1935, p. 184). The California gray whale winters and breeds in Mexico and summers in Bering, Chukchi, and Beaufort Seas. The Korean gray whale winters and breeds near Korea and summers in Okhotsk Sea (Andrews, 1914; Mizue, 1951). Resemblance of Atlantic fossils to the bones of living Pacific gray whales suggests either that Atlantic and Pacific stocks were in communication via Central America near the time of the Miocene-Pliocene boundary (Whitmore and Stewart, 1965) or via the Arctic during the Quaternary, or both. Since the gray whale will feed among ice floes, individuals must often have strayed from one ocean to the other, north of the Canadian Arctic archipelago. (For a delightful drawing of "California grays among the ice," see Scammon, 1874, plate 5.)

8. The bowhead whale *Balaena* (*Balaena*) *mysticetus* is distinctly Arctic. It summers at the edge of ice in the Arctic Ocean, and winters at the edge of ice in adjacent southern waters. Three populations are recognized. The first winters between eastern Greenland and the Svalbard Archipelago; its members were hunted almost to extermination by 1887. The second population winters west of Greenland in Davis Strait and the Gulf of St. Lawrence; a few individuals remain. The third and largest group winters in Bering and Okhotsk Seas; its members move northward and eastward through Bering Strait in April and May, and return south in autumn. (Dale W. Rice has kindly called my attention to Townsend's [1935] Map D, which indicates that Bering and Okhotsk stocks may be distinct.)

The beluga, the narwhal, and the bowhead are the only cetaceans that have solved the problem of reproducing in polar waters. The bowhead seems to be the result of an early split from right whale stock (p. 358) that has now widened to subgeneric distinction. The present tripartite North Pacific population of the right whale suggests that the split more likely took place in the Pacific Arctic than in the Atlantic Arctic. A series of Bering land bridges may have forced the issue in early Pleistocene time. During glacial maxima, the early bowheads could have taken refuge in either Pacific (Okhotsk?) or Atlantic Basins; they were subsequently free to intermingle.

PINNIPEDIA; PHOCIDAE

Udvardy (1963) developed the theme that the distribution patterns of northern pinnipeds and alcids (auks, murres, and puffins) are similar. The animals in both groups are linked to linear coastlines rather than to two-dimensional territories. The large climatic fluctuations of the Pleistocene dispersed seals and sea birds in similar fashion.

9. The harbor seal *Phoca vitulina* is circumboreal, temperature-tolerant, and nonmigratory, except in the northern part of its range, where it moves seasonally with the ice. It ranges north to Point Barrow, Ellesmere Island, and northern Norway. It has four indistinct marine subspecies; their postulated origin is outlined in Table 2. The zoogeography of the harbor seal is stressed here because it seems to exemplify the effect of alternate contraction and expansion of the polar ice sheet, a divisive effect seen also in the present distributional patterns of certain other seals.

A fifth subspecies of *P. vitulina* was proposed by Doutt (1942) to identify a landlocked form in lakes of Quebec. He wrote (p. 118): "The seals may have been isolated there for approximately 4,000 years, and it is assumed that this is the length of time which has been required to make a new subspecies."

10. The ringed seal *Pusa hispida* is circumboreal at the edge of ice, ranging to the North Pole. It is the only northern seal that keeps open holes in the ice through the entire winter. Four indistinct marine subspecies are recognized in the Arctic Ocean and in Okhotsk, Bering, and Baltic Seas, respectively. Two freshwater subspecies are recognized in Finnish lakes (Scheffer, 1958). In Bering Sea, the ringed seal drifts on seasonal ice as far south as the Pribilof Islands.

The common ancestor of the ringed seals may have been *Pusa pontica*, lectotype from the Sarmatian of Crimea, dated as late Miocene or early Pliocene (McLaren, 1960a). The taxonomy of modern *P. hispida* races is confused, mainly because of variation introduced by age, sex, and environment. Davies (1958a) made a scholarly attempt to reconstruct the Pleistocene history of the subspecies. Perhaps it is enough to state that *Pusa* is adaptable to subzero weather and to both fresh and salt water, and that its

TABLE 2. *Postulated Origin of Subspecies of the Harbor Seal* (Phoca vitulina)[1]

Years Ago	Glacial Stage	History
0–11,000	Postglacial	The subspecies *richardi, largha, vitulina,* and *concolor* as now recognized.
> 10,000	4th glacial	Four groups substantially as known today are separated: E. and W. Pacific, E. and W. Atlantic.
> 120,000	3d interglacial	The groups reunite, though distinction between Pacific and Atlantic populations persists.
> 340,000	3d glacial	Arctic ice forces seals south, separating them into Pacific and Atlantic groups (or smaller groups?).
> 420,000	2d interglacial	Easy movement around the Arctic Ocean and adjacent seas; ancestral harbor seal undifferentiated.

[1] Largely after Davies (1958a) and Ericson *et al.* (1964).

principal food (macroplankton) is widely available. Thus, Pleistocene climatic changes may have pushed ringed seals back and forth without appreciably changing their morphology.

11. The gray seal *Halichoerus grypus* is confined to the North Atlantic; it is nonmigratory and monotypic. It is represented by at least three breeding stocks: Canadian, northeastern Atlantic, and Baltic. Gray seals penetrate the Arctic to about 70° N. above Norway. Though fossil evidence is lacking, the three gray seal stocks may have separated during the late Pleistocene, always remaining within the North Atlantic basin (Davies, 1957, p. 302).

Gray seals of the British Isles, composing more than half of the world population, breed on land; others breed on ice or land. Because the gray seal everywhere gives birth to a white-coated pup, it is presumed to have originated in an icy environment. It was exposed to ice during the last glaciation and has retained a white birthcoat which can surely have no survival value today on dark-colored land nurseries.

12. The ribbon seal *Histriophoca fasciata* is monotypic and has a small range at the edge of ice in the Okhotsk, Bering, and Chukchi Seas. Its center of abundance is northwestern Bering Sea. It is regarded as one member of an allopatric pair; *Pagophilus groenlandicus* is the other. The two are the only striped pinnipeds. Because of clear taxonomic distinctions, they are thought to have split apart in early Pleistocene time. Both are strongly migratory and pelagic, and thus the confined environment of the Arctic Ocean has apparently not been attractive to them for a long time. At times in glacial cycles when the Bering and Chukchi shelves were dry land, ribbon seals may have moved into Okhotsk Sea and the deeper part of Bering Sea (Davies, 1958a, p. 107; D. M. Hopkins, written communication, 1966).

13. The monotypic harp seal *Pagophilus groenlandicus* is confined to the North Atlantic. Like the ribbon seal it breeds on ice floes, penetrating to 80° N. It has three breeding populations: White Sea, Jan Mayen, and Newfoundland. The land barrier of Greenland was responsible for the creation of slight morphological differences between the White Sea–Jan Mayen group and the Newfoundland group (Yablokov and Sergeant, 1963).

14. The bearded seal *Erignathus barbatus* is circumboreal at the edge of ice. It feeds in shallows and does not venture into the deep North Polar Basin. It has two indistinct subspecies: Pacific Arctic and Atlantic Arctic. Davies (1958a) suggested that the bearded seal was pushed south by ice and has not yet fully reclaimed areas suited to it, though King (1964) concluded that it now ranges completely around the Arctic.

15. The hooded seal *Cystophora cristata* is confined to the western

North Atlantic, at the edge of ice from Bear Island and Svalbard to eastern Canada. Though monotypic, it has two breeding centers—Jan Mayen and Newfoundland. It is a poor indicator of Pleistocene events in Bering Sea, for its geographic range is small and its ancestral affinities are with the elephant seal (*Mirounga*) of the Southern Hemisphere.

PINNIPEDIA; ODOBENIDAE

16. The monospecific walrus *Odobenus rosmarus* is nearly circumboreal. Distinct Pacific Arctic and Atlantic Arctic subspecies have long been recognized, though where they intergrade (if they do) is not clear. A recent map (King, 1964, p. 37) shows gaps in the distribution of walrus in the high latitudes of the Canadian Arctic Archipelago and Severnaya Zemlya. The walrus favors water depths of 20 to 30 meters.

Pliocene walruses are represented by *Alachtherium* from Belgium and *Valenictus* from California; also by an "odobenid, possibly new genus and species" from Santa Cruz, California, described by Mitchell (1962, p. 4). "The Santa Cruz odobenid is probably related to the ancestral stock which gave rise to the living species, *Odobenus rosmarus*" (p. 18). By implication, *Odobenus* is most likely of Pacific origin.

Pleistocene *Trichechodon,* which resembled the modern walrus but lived in warm water, is known from Florida, South Carolina, and England. *Trichechodon* and *Odobenus* coexisted in the late Pleistocene. "During the glacial period . . . both *Odobenus* and *Trichechodon* would have moved farther south, the two populations both dividing into American and European parts, and retreating again to the north during the interglacial periods" (King, 1964, p. 42).

North Temperate Marine Mammal Faunas

Species that live in temperate waters south of, and adjacent to, the Subarctic are treated lightly because they do not seem to offer good evidence concerning the Pleistocene history of Bering Strait. To judge from their present habits and temperature tolerances, some of them have never crossed the Arctic Ocean and others have never crossed in numbers sufficient to leave a trace. Where fossil records are known, they are given.

CETACEA

The dolphin *Lagenorhynchus* has distinct North Pacific and North Atlantic species. There are two of the latter, one of which is the only common dolphin north of Norway.

The Dall porpoise *Phocoenoides dalli* is a North Pacific autochthone with two forms that seem to be at least subspecifically distinct. Their ranges overlap.

The beaked whale *Mesoplodon* has distinct North Pacific and North Atlantic species, as well as species in nearly all temperate and tropical waters of the world. It is known from the upper Miocene.

The beaked whale *Berardius* ranges through most of the temperate oceans of the world except the North Atlantic. The North Pacific stock has presumably never sent an offshoot through the cold-water barrier of the Arctic Ocean; the Southern Hemisphere stock (known to be cold-adapted) has presumably never sent an offshoot northward through the warm-water barrier of the Caribbean. Of the beaked whale *Hyperoodon*, the reverse is true; it ranges through most of the temperate oceans of the world except the North Pacific.

The blue whale *Balaenoptera musculus* and sei whale *B. borealis* are cosmopolitan. They are seldom seen during summer migration as far north as Bering Strait.

The black right whale *Balaena* (*Eubalaena*) *glacialis* is represented by three subspecies in temperate waters of the North Atlantic, the North Pacific, and the Southern Hemisphere, respectively. Furthermore, Klumov (1962) concluded that the North Pacific population contains three independently migrating groups: an Okhotsk, an Asian Pacific, and an American Pacific. The northern feeding range of the right whale overlaps the southern breeding range of its relative, the bowhead, in Bering and Okhotsk Seas.

The humpback whale *Megaptera novaeangliae* is cosmopolitan. In the north it ranges to Chukchi Sea, Svalbard, and Novaya Zemlya. Specimens from the North Pacific and North Atlantic are indistinguishable.

SIRENIA, PINNIPEDIA, AND CARNIVORA

Also included in the temperate marine-mammal faunas are the Steller sea cow, two or three otariid seals, and the sea otter. Though tolerant of ice, all need ice-free shallows or shores for feeding or breeding. All belong to genera known exclusively from the North Pacific basin; here they presumably originated and here they have remained.

The Steller sea cow *Hydrodamalis gigas* was discovered on Bering Island in 1741 and was exterminated by 1768. There are no distributional records, fossil or recent, outside the Commander Islands, though a rib was picked up on Attu Island. The sea cow is the only known member of the subfamily Hydrodamalinae (Simpson, 1932, p. 424). It is the only recent sirenian living outside the tropics and the only one lacking functional teeth. It was said to feed upon seaweeds (quite certainly the kelps *Thallasiophyllum, Nereocystis, Laminaria,* and *Alaria* [Stejneger, 1936, p. 355; Scheffer in Murie, 1959, p. 367]). Reinhart (1959, p. 1) proposed that "*Hydrodamalis* is . . . on a direct line of descent from the very large Miocene *Halianassa* from California." *Halianassa* is known from both North Atlantic and North Pacific beds. Mitchell and Repenning (1963, p. 14) stated that "sirenians are found in the Eocene of the Caribbean, and apparently have continuously occupied the Caribbean since then." Only two, or perhaps three, species of *Halianassa* are known from North Pacific beds, from Mexico and California. They date from late Miocene to early Pliocene (Mitchell and Repenning, p. 15). Until evidence to the contrary is presented, I presume that ancestral sea cows entered the Pacific from the Caribbean well before late Miocene time; they came increasingly to depend upon the kelp pastures of the North Pacific; they eventually extended their range northward to the southern edge of winter drift ice; they increased in body size in response to a cold environment; they lost their teeth in response to a soft diet; and, finally, along one coast after another they succumbed to man, the hunter.

The Steller sea lion *Eumetopias jubatus* is monotypic; it breeds as far north as the Pribilof Islands and wanders to the Diomedes. Fossils are known from Pliocene (or Miocene?) beds within the geographic range of living sea lions.

Another sea lion, *Zalophus californianus,* was never tolerant of cold water and perhaps should not be listed among the north-temperate faunas. It now breeds in the Galapagos Islands, southern Japan (if not recently exterminated), and Mexico–California. It may have disappeared from the Aleutian arc when the waters chilled during late Pleistocene time.

The northern fur seal *Callorhinus ursinus* breeds only on treeless islands near the southern limit of temporary ice in Bering and Okhotsk Seas. There are no good biological reasons why it does not breed farther south. Perhaps it formerly did, and its colonies were exterminated by prehistoric man. Its main breeding grounds (Commander and Pribilof Islands) were uninhabited by man at the time of their discovery in the mid-1700's.

The range of the sea otter *Enhydra lutris* has shrunk in historic time to southern California, the Alaska Peninsula, the Aleutian, Commander, and Kurile Islands, and Kamchatka. There are no authentic fossil or recent distribution records of *Enhydra* outside the North Pacific Ocean and adjacent seas. The northern limit in historic time was the Pribilof Islands (57° N.), where life for otters must have been marginal, for drift ice frequently surrounds the islands. The oldest North American fossil is a right femur from a "presumed early Pleistocene" (*Elphidiella*) bed of coastal Oregon (Leffler, 1964, p. 53). An unerupted molar tooth from a lower Pleistocene bed of Norwich Crag, England, was assigned to *Latax* (or *Enhydra*) by Pohle, who called it "ein Mittelding zwischen *Lutra* und *Latax*" (1920, p. 167). I agree with Repenning (this volume and written communication, 1965) that *Enhydra* stock apparently originated in eastern Asia in Pliocene time. At least one branch reached the North Pacific and was successful.

Conclusion and Summary

We may assume that during each glacial stage of the Pleistocene, when a Bering land bridge appeared as a barrier to the passage of marine mammals, permanent ice over the Arctic Ocean was thick and extensive, perhaps like the fast ice of Antarctica now. V. Standish Mallory states (in ms.) that even as far south as the Strait of Juan de Fuca, shelf ice was extensive during the Wisconsin maximum. (See also Easterbrook, 1963.)

The Pleistocene series of land-and-ice barriers was effective in shaping the evolution of subspecies of beluga, ringed seal, bearded seal, walrus, harbor seal, and (?) gray whale. It may have split the common ancestor of the ribbon seal and harp seal, now subgenerically or generically distinct.

Racial differences could conceivably have arisen temporarily between North Pacific and North Atlantic stocks of the narwhal, killer whale, harbor porpoise, finback whale, and little piked whale while trans-Arctic communication was closed during the last glaciation. The time available for the evolution of differences was many tens of thousands of years. The stocks are now able to communicate more or less freely, however, and are not visibly different. We may assume that, if they deviated during the Wisconsin, they did not deviate far. (The narwhal is a special case; it presumably was not forced by ice into both Pacific and Atlantic Subarctic basins but only into the Atlantic.)

Subarctic hooded seals and gray seals are known in the North Atlantic only; no evidence exists that they have crossed the Arctic.

Known in northern temperate waters of the Pacific are six genera, represented by the Dall porpoise, Baird beaked whale, Steller sea cow, Steller sea lion, northern fur seal, and sea otter. All are unknown in the North Atlantic. Conversely, the North Atlantic bottle-nosed whale is unknown in the North Pacific. Evidence is lacking that any have crossed the Arctic during late Cenozoic time.

The inference to be drawn from the above two paragraphs is that cold water, not always coincident with ice, has acted as a barrier. It is difficult otherwise to explain the failure of certain cetaceans, sirenians, and seals to cross the Arctic during interglacial periods, at least one of which may have lasted half a million years (Ericson *et al.*, 1964).

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GROWTH LAYERS IN TEETH OF SUCKLING FUR SEALS

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In the fur seal, *Callorhinus ursinus,* the roots of the permanent upper canine teeth begin to form near time of birth. During the next 16 weeks, about 10 or 11 layers of dentin are laid down, each representing one period of suckling, followed by a fast. The layers demonstrate a relationship between feeding and growth of teeth.

INTRODUCTION

Coarse layers in the roots of fur seal teeth correspond in number to the age of the animal in years (Scheffer, 1950a). Finer layers, located between the annual layers, were observed by Scheffer and Kraus (1964, p. 309). On a gelatin impression of the tooth of a yearling seal, they counted 11 layers on the portion of the root first deposited, plus 5 narrower layers deposited later, plus a series of even narrower, poorly defined layers continuing to the apex of the root. They did not know what environmental factors contributed to the formation of the layers, but theorized that they "originate in individual periods of intensive feeding." Now we correlate the 11 first-formed layers with the nursing cycles of the young seals.

A nursing cycle (with respect to *Callorhinus*) is defined as a period of time during which a lactating female and her suckling pup remain together on land, plus a subsequent period of separation when the pup is left alone on land while the female goes to sea to feed. For several hundred marked females and pups at St. Paul Island, Alaska, the average length of the initial, or perinatal, cycle was 15.4 days, consisting of 8.0 days together, followed by 7.4 days apart (Peterson, 1965). Lengths of cycles subsequent to the initial one were quite uniform, averaging 11.4 days—2.0 days together and 9.4 days apart.

The mean birth date of pups in 1962 and 1963, as calculated from daily censuses, was 7 July. The mean date of last nursing, from records of marked animals, was 8 November. During the 4-month interval, marked females and pups completed an average of 10.9 nursing cycles.

METHODS

To test for possible correlation between the number of nursing cycles and the number of layers in the teeth, we examined the right upper canines of 31 seals of ages between full-term fetal and 4 years. The teeth had been held in dry storage, either loose or in museum skulls. Unfortunately, none were representative of ages 5 to 6 months, the critical weaning and post-weaning periods in November and December. Each tooth was: (1) examined under a 10 × dissecting microscope; (2) photographed at 5 ×; (3) partly decalcified (cleared) by macerating for 10 days in EDTA (ethylenedinitrilotetracetic acid, 41.3 g.; sodium hydroxide, 4.4 g.; water to make 1 liter; resulting pH about 7.4); (4) re-examined under a dissecting microscope; (5) stored in 50% isopropanol with a little glycerin.

We made root-surface casts in agar gel (3%) or gelatin (10%) of several teeth and photographed the resulting microrelief at × 5 or × 10. We cross-sectioned the tooth of a 3-year female in a search for layers which would have persisted from the suckling period.

ROOT DEVELOPMENT IN RELATION TO AGE AND NUTRITION

Evidence on the growth of the root is summarized below.

In one full-term and three newborn pups taken 24 June to 10 July, the crown was about 14 mm. long, measured along the posterior (distal) surface. The root had not begun to form in two specimens and was barely forming in the other two.

In pups of various ages from 23 to 103 days, as many as 10 layers were counted on the roots. Although layers could be seen in good illumination on the roots of all these teeth, the layers nearest the crown (earliest formed) were usually obscure. On the basis of teeth from three male and three female pups, with well-defined layers, we estimate that the average length (parallel to the axis of the tooth) of a layer on the male tooth is 0.3 mm. and growth in length of the root during the entire nursing period is 3-4 mm.; for females, the estimates are 0.4 mm. and 4-5 mm.

In 1965, M. C. Keyes (Marine Mammal Biological Laboratory) attempted to raise fur seal pups on artificial formulas. He captured a female on 20 July at estimated age 1 to 3 days and fed her almost daily until she died on 16 December at age 150 to 152 days. She weighed 5.8 kg. at the start of the experiment and 4.0 kg. at death. Her

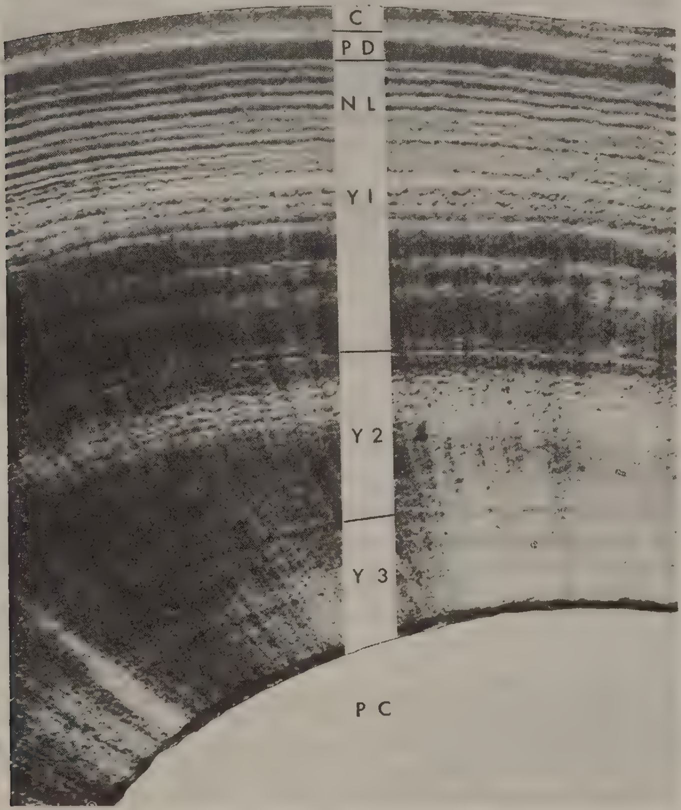

FIGURE 1

Cross section of fur seal tooth showing nursing layers in dentin. Right upper canine of known-age (tagged) 3-year female killed 11 August 1958; thin section of root about 5 mm. from crown-root junction; in oil with refractive index 1.560; transmitted light; × 50. C = cementum, PD = prenatal dentin, NL = nursing layers; Y 1, 2, and 3 = middle regions of years 1, 2, and 3; PC = pulp canal.

right upper canine was about the same size as that of a wild female killed at age 92 days, though it lacked the typical growth layers. The root had two broad layers; the one deposited first was 2.6 mm. long and the other was 2.1 mm. The later layer was faintly subdivided into two parts. The feeding schedule was: 45 days on a casein formula, 49 days on a fish-flour formula to which chopped fish was gradually added, and 53 days on fish.

Six yearling seals (two males and four females), of estimated ages 7 to 8 months, were picked up dead or dying on Oregon and Washington beaches in January and February 1950 (Scheffer, 1950b). One female weighed only 5.2 kg., or less than the weight of some newborn pups. On the teeth of two males where layers were fairly distinct, we counted 14 or 15 layers.

The root of the canine of a healthy male about 16 months old, killed on St. Paul Island in November, showed two series of layers. The older series included 13 or 14 layers; the younger series an indeterminate number.

In the canine of a 3-year female, the dentin which had been deposited in early postnatal life showed 10 or 11 distinct layers (Figure 1).

Conclusions

We conclude that each layer in the root of the tooth of the suckling fur seal represents one nursing cycle. The rhythm of nursing cycles is regular. An average of 10 or 11 bands, representing cycles of 11 days each, are deposited during the 16-week nursing period.

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Advances in the Off-bottom Culture of Oysters

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Abstract

For the past 10 years the Bureau of Commercial Fisheries has been experimenting with off-bottom culture of oysters, *Crassostrea virginica*, along the east coast of the United States. Earlier studies at Cape Cod, Massachusetts, demonstrated that when oysters are suspended off-bottom growth, survival, and quality are improved.

Further studies in Chesapeake Bay have shown that excellent oyster sets can be obtained by suspending shells from rafts. In one area in 1965 more than 20 oyster spat per shell were collected on suspended shells, as compared with 5 spat per shell for shells on the bottom.

Other studies now in progress at Oxford, Maryland, include the off-bottom culture of oysters in natural and man-made ponds. Preliminary findings indicate that natural ponds are excellent for growing and fattening oysters, and artificial ponds can be used to produce seed oysters. On the basis of recent research, the off-bottom culture of oysters appears to have commercial application along the Atlantic coast.

INTRODUCTION

The present decline in the oyster industry along the east coast of the United States is well known (Galtsoff, 1956; Shaw, 1962; Engle, 1966). For example, in Chesapeake Bay, the major oyster producing area in the nation, production today is only about 10 percent of that in the early 1900's (Engle, 1966). To attribute this decline to one major cause is impossible and unrealistic. Such factors as poor bottom, overfishing, predation, disease, pollution, and hurricanes are a few in an endless list of causes of decline.

One of the most significant reasons for a failing industry is the lack of private farming. Up to the late 1800's no economical need for oyster farming existed. Oysters were freely accessible and abundant in most coastal estuaries. Unfortunately, as the demand for oysters increased in the 20th century the natural populations were reduced beyond their ability to repopulate. Thus, the eastern oyster has slowly begun to disappear—first in Maine, New Hampshire, and Massachusetts, then in Long Island Sound and Delaware Bay, and more gradually in Chesapeake Bay. The disappearance of oysters left many of the natural bars barren, and the bottoms are no longer suitable for oyster production. Unless modern oyster-farming techniques are put into practice oyster populations will become further reduced along the Atlantic coast.

Glude (1966) stated, "The difficulty of obtaining exclusive use of oyster lands (in the Maryland portion of Chesapeake Bay) has prevented development of private oyster farming". The major oyster bottoms in Maryland are public domain. Private leases are few and many are located where bottoms are unproductive. At this time the chances appear very slim that private leasing will increase. Most watermen oppose the leasing of a single acre of public bars for private use. The rights to farm oysters on good bottom are accordingly limited; the industry must continue its present decline unless some innovation appears. Possibly off-bottom oyster culture can help revolutionize the industry. This method of culture can open up many areas remote from public bars.

OFF-BOTTOM OYSTER CULTURE IN JAPAN

The Japanese began to experiment with off-bottom oyster culture in the late 1920's (Cahn, 1950). Seno and Hori (1927) determined that suspended oysters were fatter and grew faster than oysters growing on the bottom. Now over 90 percent of the oysters harvested in Japan are grown off-bottom (Glude, 1964). Rows of rafts carrying either strings of shells to catch seed or strings of oysters being grown to market size are found in many of the inlets and bays of Japan. Along the shore are rows of racks on which strings of seed are suspended for hardening.[1] A portion of this seed is shipped to the west coast of the United States. The success of off-bottom oyster culture in Japan represents the true farming of a sea product.

Among the factors that contribute to Japan's success in off-bottom oyster culture are: a need for high-protein food; a limited bottom zone suitable for growing oysters; and low labor costs. In the United States the reverse is true. High-protein food is abundant; good, potential bottom for growing oysters is extensive (though many acres are not available for private leasing); and labor costs are high. Off-bottom culture of oysters, therefore, has been limited in this country.

OFF-BOTTOM CULTURE IN THE UNITED STATES

Several recent developments have stimulated off-bottom oyster culture. As the landings have declined the demand for oysters has increased, and so has the price. In areas such as New England the demand and price have risen enough to make off-bottom oyster culture practical. At Fishers Island, New York, shells are suspended from rafts to catch seed oysters which are later sold to planters of Long Island (Binmore, 1964; Matthiessen, 1965). Similar methods are used in the State of Washington (Steele, 1964).

THE BUREAU'S RESEARCH IN OFF-BOTTOM OYSTER CULTURE

The Bureau of Commercial Fisheries began extensive studies in 1956 on the feasibility of growing oysters to market size by suspending them from rafts. The experiments are well documented (Shaw, 1962, 1963, 1965; Shaw and Mc Cann, 1963). These off-bottom studies at Cape Cod, Massachusetts, led to the following conclusions: (1) growth was almost twice as fast; (2) meat quality (percentage solids) was improved; (3) mortality was reduced because oysters were out of reach of many predators; (4) areas unsuitable for oyster culture because of poor bottom were made available; (5) more oysters could be grown per unit of area; and (6) growing of oysters on rafts appeared to be commercially feasible.

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[1] In hardening, oysters are exposed to air for many hours each day. The process conditions them for shipment to other countries.

Research in off-bottom oyster culture has been conducted the past several years at the Bureau of Commercial Fisheries Biological Laboratory, Oxford, Maryland. Some of these studies are unique for the United States. The research can be listed under three projects: (1) rafting of shells in natural waters for seed production; (2) off-bottom culture in artificial ponds; and (3) growing seed off-bottom to market size in a natural pond. Certain of these studies are so new that findings thus far are only preliminary.

Rafting of Shells for Seed Production

In the summer of 1965 five styrofoam rafts containing shell strings and bags of shells were moored in Broad Creek on the eastern shore of Chesapeake Bay, Maryland (Fig. 1). The setting on all shells was heavy (average of 25 live spat per shell), as compared with shells planted on the bottom (5 spat per shell). In 1966 the Maryland Department of Chesapeake Bay Affairs rafted 1,000 bushels of shells in St. Mary's River on the western shore of Chesapeake Bay, Maryland, (Fred W. Sieling,

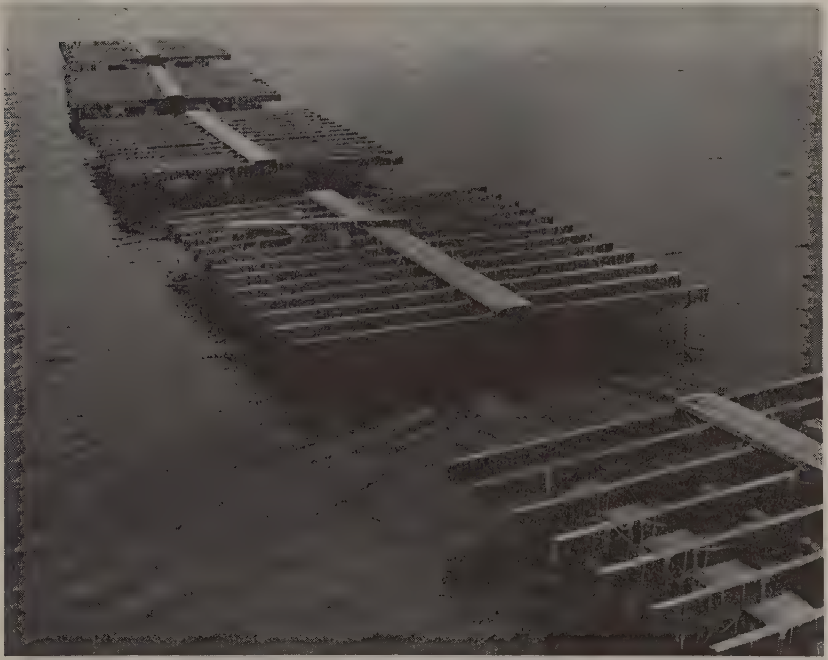

Fig. 1. Styrofoam rafts in Broad Creek, eastern shore of Chesapeake Bay, Maryland. Strings and bags of shells are suspended from rafts to catch seed oysters.

personal communication). Counts on the suspended shells were estimated to be over 3,000 spat to the bushel. (A count of 500 to a bushel is commercially acceptable in Maryland). The results of these two experiments, which I believe represent the first attempts to obtain seed on shells suspended from rafts in Chesapeake Bay, could mark the beginning of an expanded raft system in the bay for seed production. Similar studies are now being conducted by the Bureau of Commercial Fisheries in Tampa Bay, Florida; by the Alabama Department of Conservation, Seafood Division, in Mobile Bay (Smith, 1966); and by the State of Maine in Spinney Creek and Piscataqua River (Anonymous, 1966).

Off-Bottom Oyster Culture in Artificial Ponds

Four quarter-acre artificial salt water ponds were constructed at the Oxford Laboratory in the fall of 1964 (Fig. 2). The ponds are nontidal; water is pumped into them through a dual sea-water system. The depth (maximum 3¼ feet) of each pond is controlled by a series of baffles; the ponds can be drained in 24 hours by removing all baffles. Thus many environmental factors such as temperature, salinity, and animal life can be controlled.

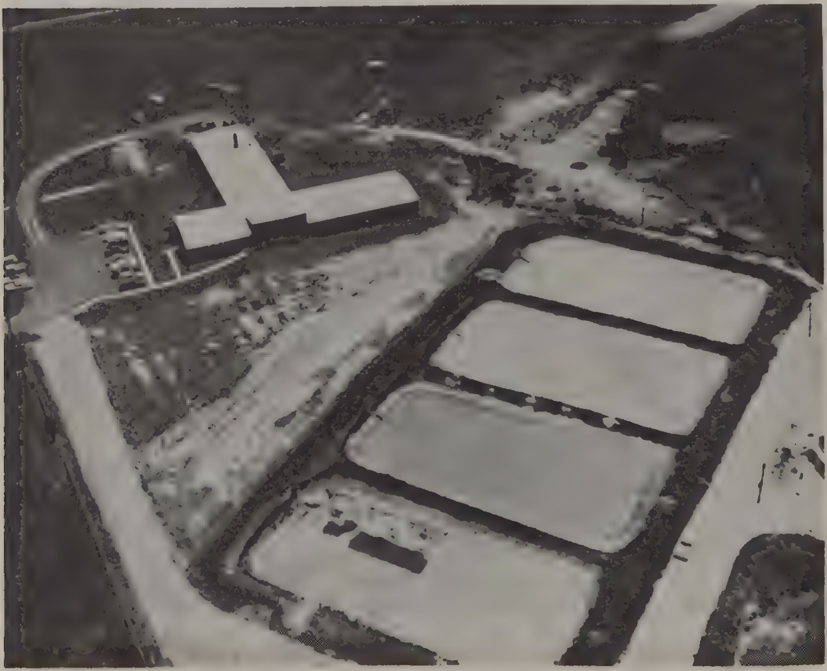

Fig. 2. Four ¼-acre artificial salt water ponds, Oxford, Maryland.

An early study was the comparison of growth and condition of seven strains of oysters suspended from rafts in an artificial pond and a natural pond. All strains grew at about the same rate in both environments (Table I). Meat quality (percentage solids) was higher in the natural pond — an indication that the oysters in the artificial pond were receiving less food. New feeding experiments in which commercial fertilizer is applied to increase phytoplankton are now underway in an attempt to improve the condition of oysters in the artificial pond.

TABLE 1

FINAL MEAN HEIGHT (MILLIMETERS) AND PERCENTAGE OF SOLIDS FOR EACH STRAIN OF OYSTERS GROWN IN AN ARTIFICIAL POND AND A NATURAL POND, MARCH 1966. COMPARATIVE STUDY INITIATED AUGUST 1964.

	Boone Creek (natural pond)		Quarter-acre artificial pond	
Strain	Mean Height	Percentage Solids	Mean Height	Percentage Solids
Harris Creek	81.7	16.2	76.7	8.2
Eastern Bay	79.8	15.5	75.8	9.4
St. Mary's River	79.5	16.6	74.0	9.9
Little Choptank (Town Point)	85.0	16.6	78.5	10.1
Little Choptank (Cedar Point)	82.0	17.5	75.8	10.5
Tar Bay	79.9	17.0	78.2	10.1
Broad Creek	79.7	15.9	75.8	8.6

Another study being conducted in the artificial pond is the production of seed oysters. Several hundred strings of shells were suspended from five rafts, similar to those used in Broad Creek, in one pond. In June 1966 the water flow was stopped and the outlet plugged. Over 4 million larvae, reared to the straight-hinge stage in the laboratory, were placed in the pond. About 10 spat per string of 30 shells were caught in this completely artificial culture of seed oysters. In 1967 we plan to add over 10 million larvae to the pond to increase the setting intensity.

It is too early now to say that artificial ponds can be used commercially for seed production and rearing of oysters, but preliminary results of studies now underway have been promising.

Growing Oysters to Market Size from a Rigid Structure

The commercial feasibility of growing oysters off-bottom in a natural pond is being tested at Oxford. Over 2,000 strings of seed oysters representing three year classes (1963, 1964, 1965) have been suspended from a rigid structure in Boone Creek, a natural pond adjacent to the laboratory. Each string contains 30 shells and the shells are 1 inch apart. The rigid structure is 108 x 12 feet (Fig. 3). Two rows of pilings are joined by 1- by 10-inch crossbars. Resting on each pair of crossbars are five 4- by 4-inch boards. Rows of staples (3 inches apart) lie along opposite sides of the 4 by 4. One string is attached to each staple (Fig 4). The first crop of oysters will be harvested this winter (1963 and 1964 year classes), and the second crop in the winter of 1967-68 (1965 year class).

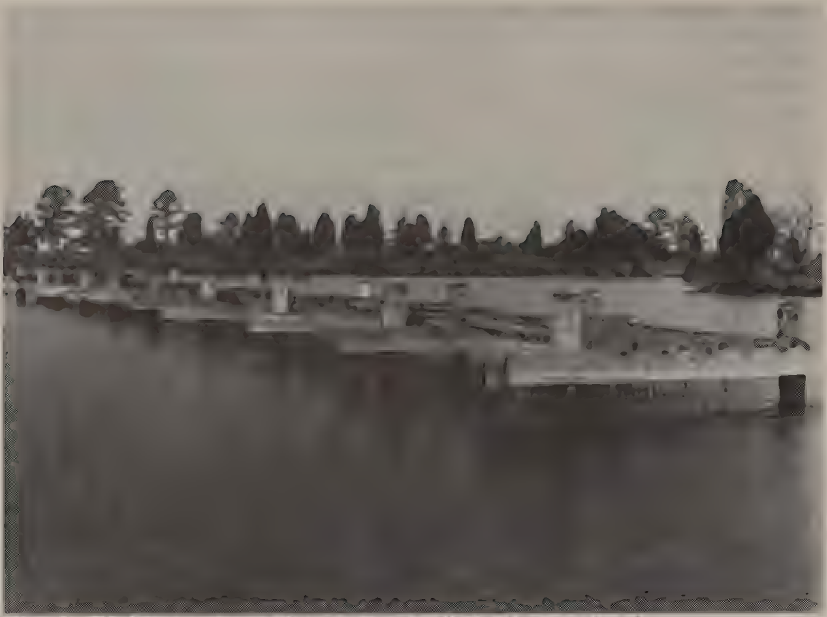

Fig. 3. Rigid structure, Boone Creek, Oxford, Maryland.

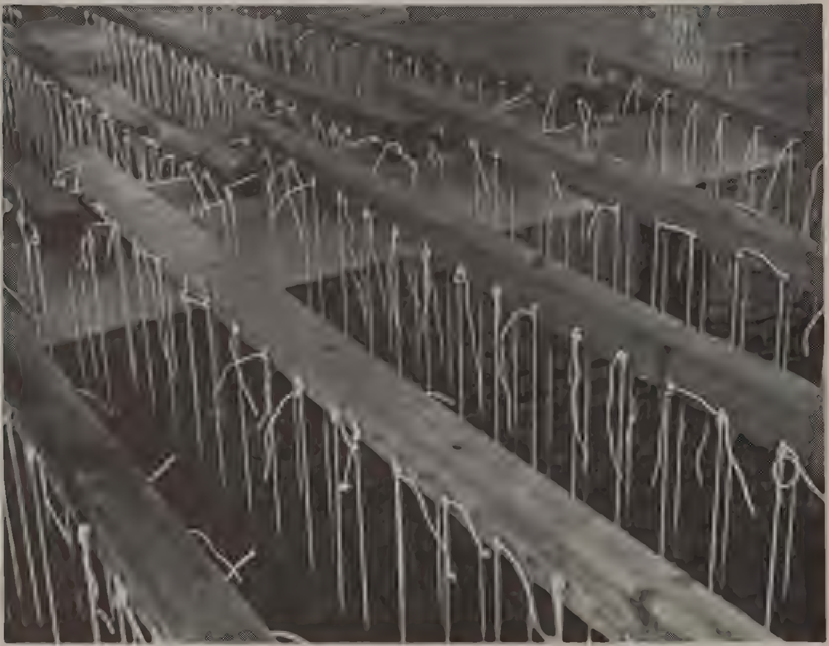

Fig. 4. Close-up showing attachment of strings to rigid structure.

Since the oysters are being grown in low-salinity water (12-16 ppt) their market value is less than that of oysters grown in saltier water. Experiments are underway to test the effects of salinity by transfer to Chincoteague Bay where the salinity averages about 30 ppt. Every 4 months samples of the suspended oysters are moved to trays in the bay (Castagna, 1964). This process, known as "salting", doubles the oyster's value. Preliminary transfers from low to high salinity have been highly successful, and growth has been excellent. A careful evaluation of the cost of transferring oysters on a commercial scale will have to be made before recommendations can be offered.

THE FUTURE OF OFF-BOTTOM OYSTER CULTURE

We are now in a period where breakthroughs in the off-bottom culture of oysters are being made in the United States. The advances are not new. The Japanese obtained faster growth, fatter oysters, lower mortality, and greater yields per unit of area in the 1920's when they began culturing *Crassostrea gigas* off the bottom. We are simply repeating their studies with a different species, *C. virginica.*

As stated earlier the stimulus that induced the Japanese to change from bottom to off-bottom culture has not, until recently, been transmitted to the oyster industry of the United States. With greater demand for seed oysters and for high quality market oysters, a major change in culture techniques is indicated. In the future we visualize fleets of rafts carrying shells to catch oyster larvae. After setting, the seed could be planted on private leases or grown off-bottom in protective ponds and coves. Numerous shellfish hatcheries, similar to those described by Loosanoff and Davis (1963), would be located in areas of poor natural setting. The seed produced in these hatcheries would be utilized by the oyster growers of the area.

On the west coast the oyster industry has depended on the importation of Japanese seed. The cost of broken Mijagi seed has steadily increased from $3.50 per case (2.4 bushels) in 1930 to $9.50 per case in 1960 (Steele, 1964). In 1965 oyster seed production in Japan was a near failure; hence the number of cases imported into the United States was reduced. Because of the higher costs of imported seed and the possibility of further failure setting in Japan, members of the west coast oyster industry may have to produce their own seed. Several areas in the State of Washington and in Canada, if developed, could supply enormous quantities of seed if techniques of off-bottom rearing were applied.

It is more difficult to comment on the future of off-bottom culture in the Gulf States. Research has just been initiated in this area; the development of off-bottom oyster culture will depend on the outcome of these studies.

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Seasonal Fouling and Oyster Setting on Asbestos Plates in Broad Creek, Talbot County, Maryland, 1963–65

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Seasonal Fouling and Oyster Setting on Asbestos Plates in Broad Creek, Talbot County, Maryland, 1963–65

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ABSTRACT: Weekly setting frequencies of oysters, bryozoans, barnacles, mussels, and flatworms were observed in Broad Creek, Talbot County, Maryland, during 1963, 1964, and 1965 on asbestos-plate collectors. Except for an early oyster set in 1965, all species set in greatest numbers at approximately the same time in a given year, but the height of the peak of setting intensity varied from year to year.

Oysters and mussels were more abundant on the undersurface when collectors were 4 inches apart, and on the upper surface when they were 1 inch apart. Setting of barnacles, bryozoans, and flatworms was greater on the undersurface of all plates. In one year of testing (1963), oyster setting was similar on shells and plates.

It is recommended that shells be planted in Broad Creek during the first week of July to catch seed oysters.

Introduction

Since 1961 the seasonal setting of the American oyster *Crassostrea virginica* has been monitored in tributaries near Oxford, Maryland (Shaw, 1966). The setting of the following five fouling organisms has also been recorded: two species of encrusting bryozoans, *Electra crustulenta* and *Membranipora tenuis;* the barnacle *Balanus improvisus;* the hooked mussel *Brachidontes recurvus;* and the flatworm *Stylochus ellipticus*. The first four fouling organisms compete with oysters for space (Beaven, 1947) and the flatworm preys on young oyster spat (Loosanoff, 1956; Webster and Medford, 1961).

This paper describes the seasonal setting of oysters and associated fouling organisms in Broad Creek, Talbot County, Maryland, in 1963–65. Data are given on the percentage of animals setting on the undersurface and upper surface of test plates. From the knowledge gained, it may be possible to plant shells at the proper time to obtain maximum oyster setting and reduce fouling and predation.

Area of Study

The oyster setting potential of five adjacent tributaries—Harris Creek, Broad Creek, Irish Creek, Boone Creek, and Tred Avon River (Fig. 1)—has been investigated for the past several years. Since Broad Creek was found to have a higher rate of oyster setting than the other four streams, only the setting in this tributary is discussed.

Broad Creek is a shallow body of water with a maximum channel depth of 35 feet. The creek has 4,000 acres of natural oyster bottom of which 2% (80 acres in 1966) have been reserved for seed production by the Maryland Department of Chesapeake Bay Affairs. Each spring dredged shells are planted on the reserve. Setting occurs during the summer. The following spring the shells, with attached spat, are placed on adjacent bars.

From June to October, in the 3-year period, the water temperature in Broad Creek at station 5 (Fig. 1) ranged from 17.8 to 29.0 C and the salinity from 10.2 to 17.8‰ (Fig. 2). Dissolved oxygen, monitored only in 1963, was near saturation at all times. Mean range of tide was 1.4 feet.

Results

SAMPLING STATIONS AND OBSERVATIONS

At each monitoring station three wooden poles were driven into the bottom and joined together about 5 feet above the water's surface to form a tripod. A plate holder (Fig. 3) was suspended 1 foot off bottom from each tripod. Two asbestos plates (4¾ inches square), previously seasoned in seawater for 1 week and then scraped clean, were exposed at 1-week intervals from 14 June to 2 October 1963 at 4 stations; from 10 June to 23 September 1964 at 7 stations; and from 1 June to 21 September 1965 at 13 stations. Previous weekly monitoring in Boone Creek (Fig. 1) indicated that except for a May set of barnacles very little fouling and no oyster setting occurred before June or after September.

All animals, on a central $100\ \text{cm}^2$ area, were counted on the undersurface of the top plate and the upper surface of the bottom plate. Plates were 4 inches apart in 1963, and 1 inch apart in 1964 and 1965. Average weekly abundance, for each species, was determined by dividing the total count on all plates by the number of plates. The annual total of each species found on the undersurface was compared with the annual total of the same species on the upper surface.

WEEKLY FLUCTUATIONS IN SETTING

Figures 4 to 8 show the weekly fluctuations of setting for oysters, bryozoans (2 species combined), barnacles, mussels, and flatworms for 1963, 1964, and 1965. All species except mussels had greater setting intensity in 1963 during the week of 31 July

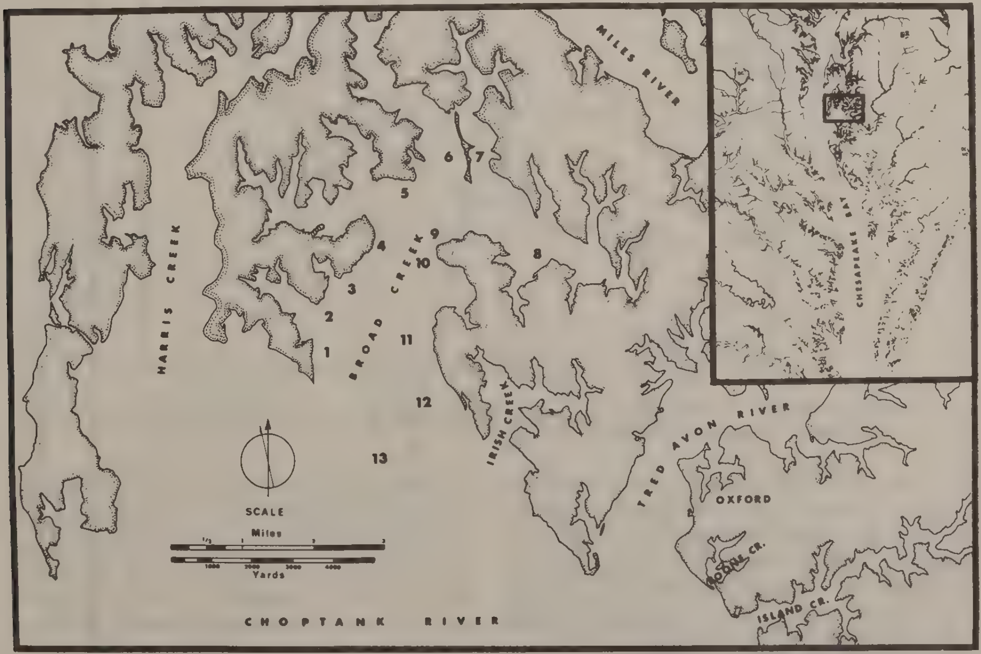

Fig. 1. Study area—stations 1, 5, 8, and 9 were monitored in 1963; stations 1, 2, 5, 6, 7, 8, and 9 in 1964; and stations 1 to 13 in 1965. The insert indicates the location of the area in Chesapeake Bay.

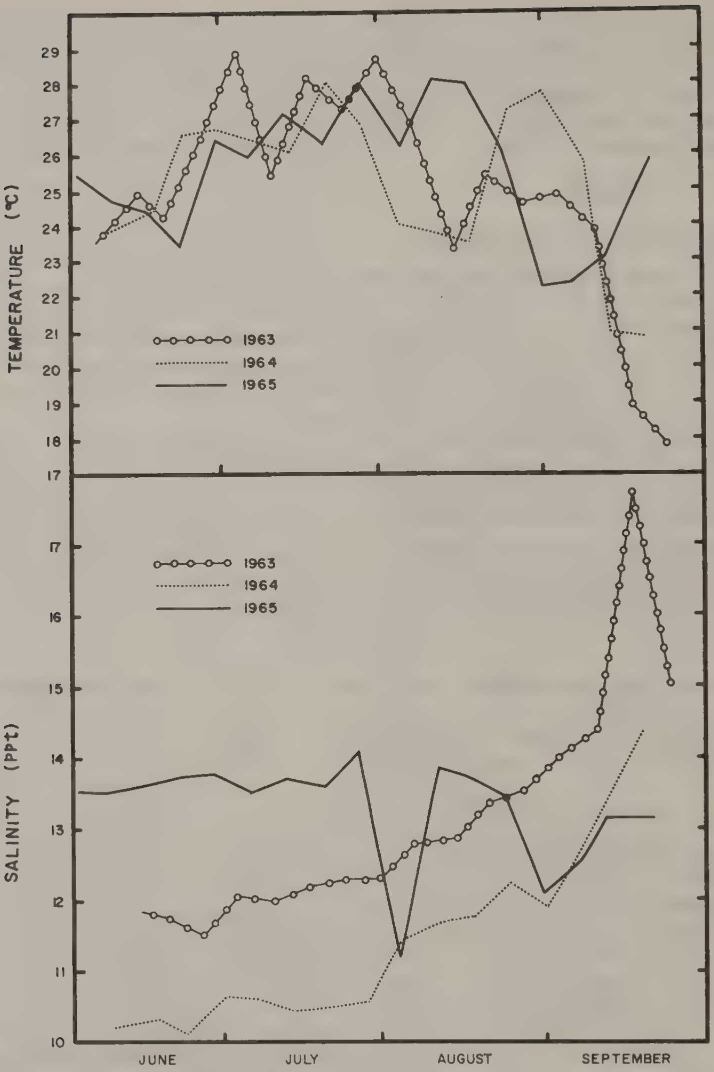

Fig. 2. Weekly fluctuations in temperature and salinity from June through September for 1963, 1964, and 1965 in Broad Creek, Maryland.

to 7 August. The peak of mussel setting occurred a week earlier, 24 July to 31 July. In 1964, the height of setting intensity came between 23 June and 7 July, approximately a month earlier than in 1963. A second wave of oyster and mussel setting occurred between 27 July and 4 August. Setting in 1965 fluctuated considerably during the 4 months. With the exception of oysters, major setting was between 3 August and 17 August. A second peak of bryozoan setting took place between 31 August and 7 September. The major peak of oyster setting in 1965 was between 22 June and 13 July (Fig. 4) and a smaller peak appeared when the other species were having their major wave of setting.

On the basis of the total number of animals per plate per week, oysters set most heavily in 1965, bryozoans in 1963, mussels in 1964, and flatworms in 1963; barnacles set at about the same intensity for all three years.

SETTING ON UNDERSURFACES AND UPPER SURFACES

The percentage of animals setting on either the undersurface or upper surface during 1963, 1964, and 1965 varied with the distance between plates (Table 1). In 1963 when the plates were 4 inches apart, oyster setting was greater on the undersurface (60.5%), but in 1964 and 1965 when the plates were 1 inch apart, more oysters were found on the upper surface (78.0 and 80.4%, respectively). Barnacles, bryozoans, and flatworms were in greater numbers on the undersurface; the change in distance between plates had little effect. When the plates were 4 inches apart (1963), 45.3% of mussels were on the upper surface, but more than 85% were on the upper surface when 1 inch apart (1964 and 1965).

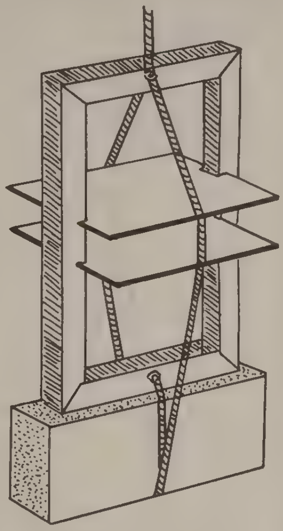

Fig. 3. Plate holder.

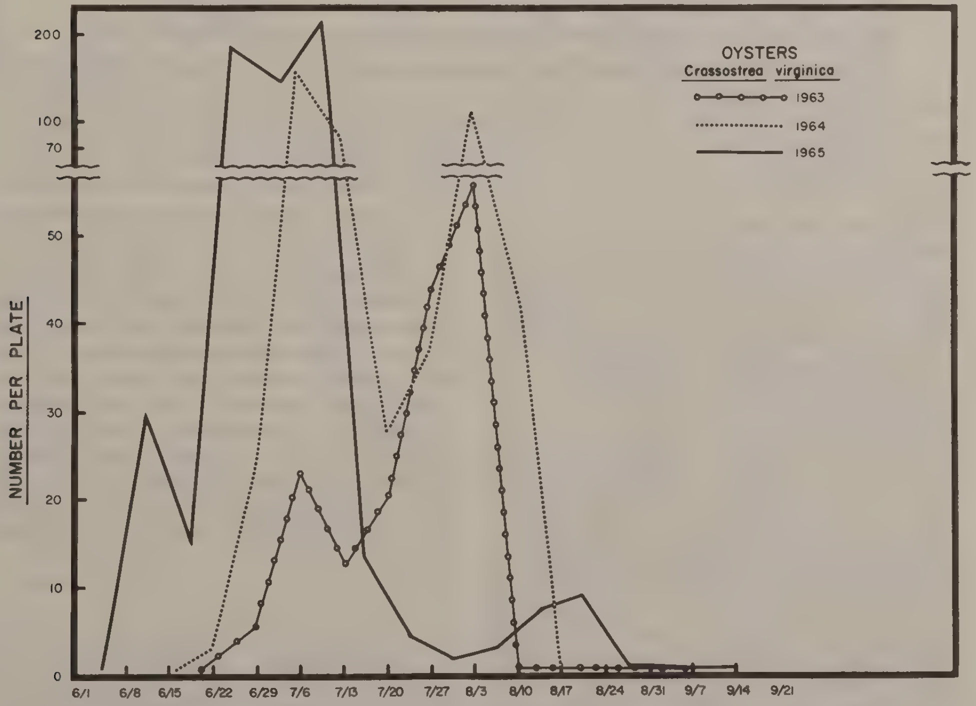

Fig. 4. Weekly fluctuations of setting on asbestos plates for oysters for 1963, 1964, and 1965 in Broad Creek. Weekly counts represent the average number of animals per plate.

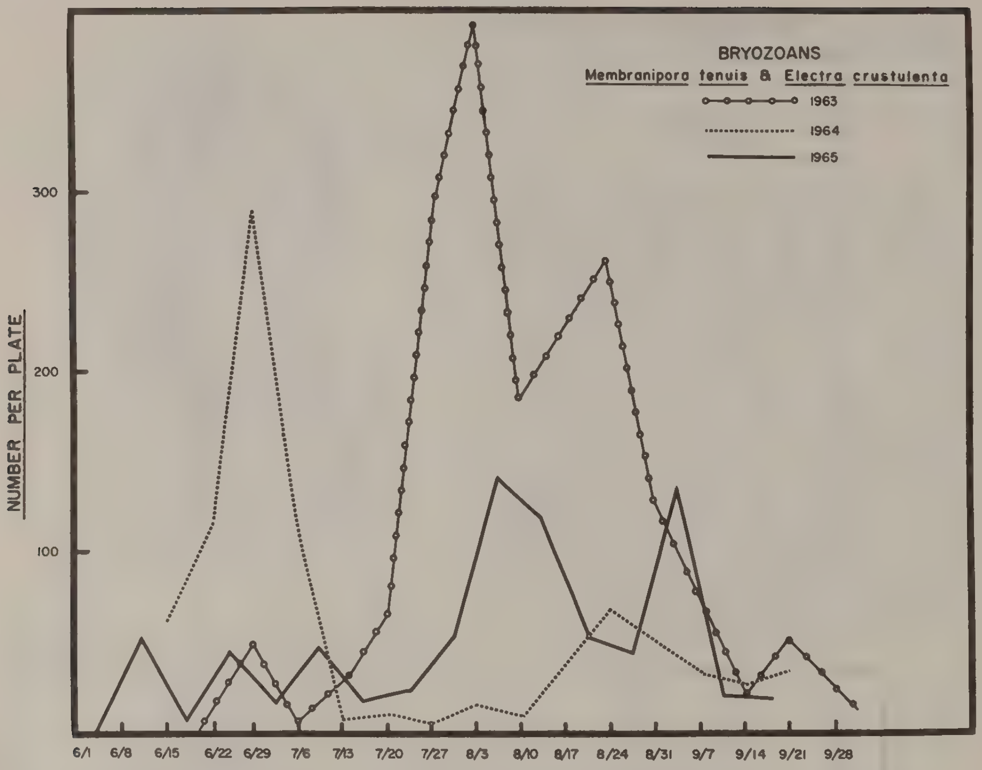

Fig. 5. Weekly fluctuations of setting on asbestos plates for bryozoans (2 species combined) for 1963, 1964, and 1965 in Broad Creek. Weekly counts represent the average number of animals per plate.

SETTING ON PLATES AND OYSTER SHELLS

The use of asbestos plates was a departure from the usual method of assessment from setting on oyster shells (Andrews, 1951, 1955; Beaven, 1955). Butler (1954) used asbestos plates ("cement board") because a selected area of a flat surface could be examined easily.

In 1963, a weekly comparison was made on the setting of oysters on plates and shells at four stations in Broad Creek (Fig. 1). Plates were suspended in the manner previously described (Fig. 3). Suspended alongside the plates was a chicken-wire bag containing 12 shells with their inner faces up, and 12 shells with their inner faces down. Both plates and shells were changed weekly. One hundred square centimeters on each plate and about 50 square centimeters of the inner face of each shell were examined for oyster spat. The average number of spat per plate was compared weekly with twice the average number of spat per shell. This procedure provided an approximately equal-area comparison between plates and shells.

The weekly frequencies are shown in Figure 9. Setting on both collectors reached an initial peak between 3 July and 10 July; and a major peak appeared between 31 July and 7 August. On the basis of the similarity of trends in setting on shells and plates, the use of shells to monitor weekly intensity of oyster setting was discontinued after 1963.

APPLICATION OF FINDINGS TO OYSTER MANAGEMENT

The orientation of surface has been found to affect the setting of oysters and other sessile organisms. When flat collectors were oriented in a plane horizontal to the bottom,

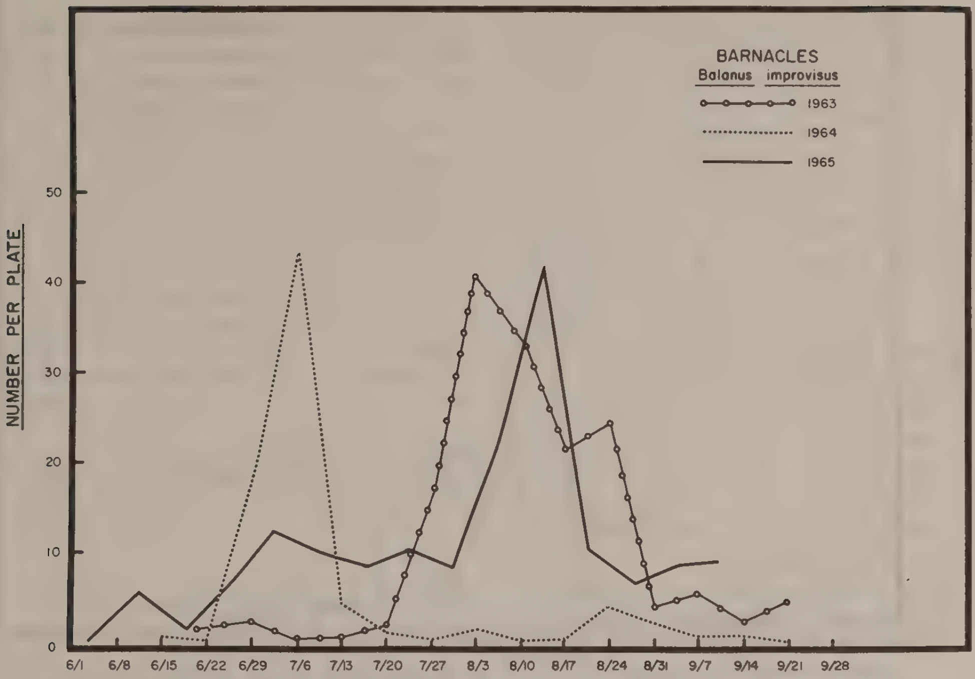

Fig. 6. Weekly fluctuations of setting on asbestos plates for barnacles for 1963, 1964, and 1965 in Broad Creek. Weekly counts represent the average number of animals per plate.

most intensive setting was on the upper or the lower surface, depending on geographic region and experimental conditions. Butler (1954) observed more oysters on the upper side of plates when collectors were placed near the surface of the water, but on the lower side when the collectors were placed near the bottom. Of 11 other investigations, some of which concerned species of oysters other than *Crassostrea virginica,* 8 showed that oysters set in greater numbers on the undersurface, and 3 showed a more abundant set on the upper surface (Table 2).

McDougall (1943) and Fuller (1946) found that barnacles attach in greater number on the undersurface, but Pomerat and Reiner (1942) observed that barnacles settled irregularly in relation to surface angle. McDougall (1943) also observed that bryozoans set more heavily on the undersurface. Fuller (1946) reported that the count of mussels was higher on the upper surfaces in 7 experiments and higher on the undersurfaces in 18.

Orientation of setting surface is probably only one of many factors contributing to the setting behavior of metamorphosing larvae. When the distance between plates was reduced from 4 inches to 1 inch, the greatest percentage of oysters and mussels shifted from the undersurface to the upper surface. Other factors such as siltation, fouling, light, currents, gregariousness, type of surface, color of surface, and swimming position of larvae when setting have all been reported to affect setting. Galtsoff (1964) stated, "...it is impossible to ascertain the effects of a single factor of the environment while testing under complex and variable natural conditions."

The period of cultch exposure to catch oyster spat is extremely important: collectors set out too early can become so silted or covered with fouling organisms that oyster setting is reduced (Beaven, 1947), and collectors put in place too late miss many of the metamorphosing oyster larvae. Oyster setting in Broad Creek is rarely of commercial importance before 1 June or after 1 September. In two of the three years

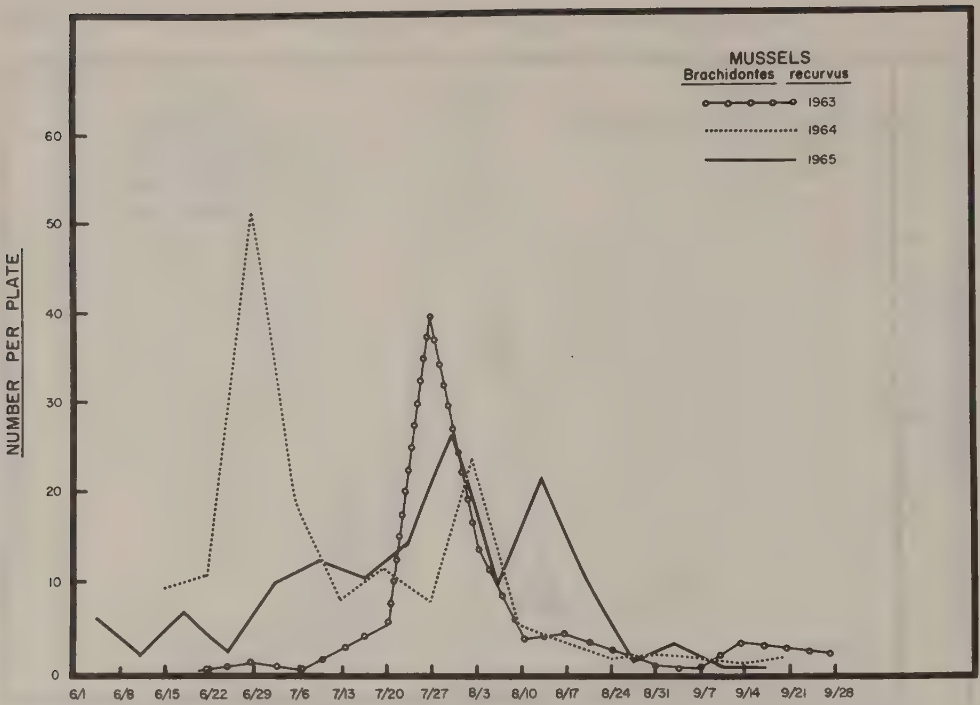

Fig. 7. Weekly fluctuations of setting on asbestos plates for mussels for 1963, 1964, and 1965 in Broad Creek. Weekly counts represent the average number of animals per plate.

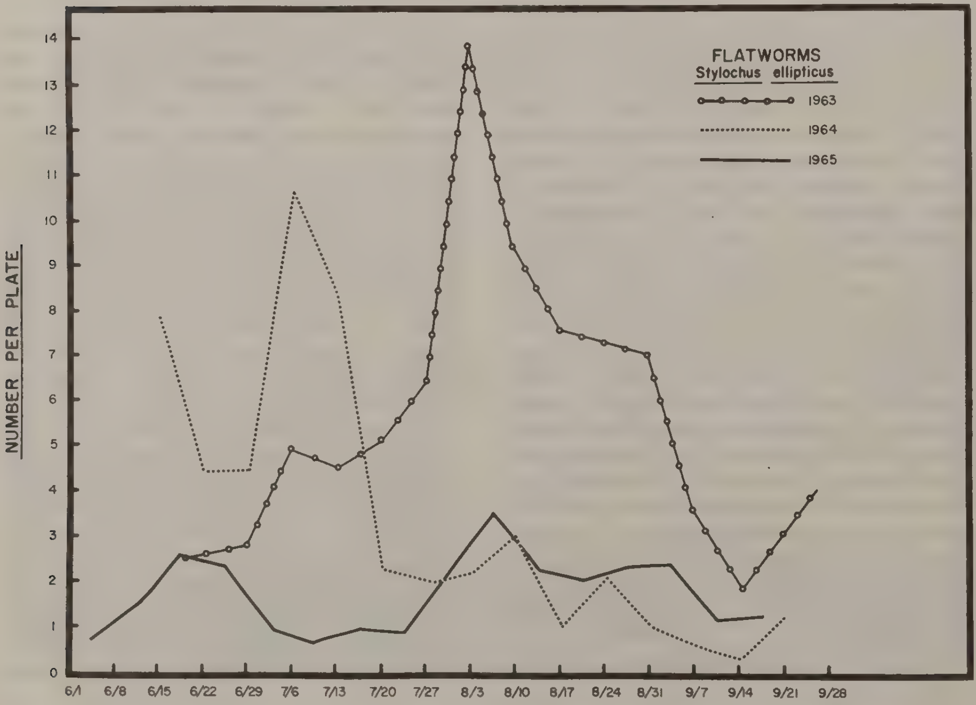

Fig. 8. Weekly fluctuations of setting on asbestos plates for flatworms for 1963, 1964, and 1965 in Broad Creek. Weekly counts represent the average number of animals per plate.

of monitoring, major oyster setting occurred after 1 July. Although heavy setting took place before 1 July 1965, much oyster setting also occurred after this date.

Except for the early oyster set in 1965, fouling organisms and oysters set at about the same time, but the major peak of setting varied from year to year. Fouling, therefore, cannot be completely eliminated by proper timing of shell exposure. The use of chemicals (polystream and drillex) to reduce fouling was unsuccessful in these waters (Shaw and Griffith, 1967). Even though fouling cannot be prevented, the correct exposure of shells at the peak of oyster setting will prevent the collectors from being covered by the growth of organisms that have set earlier in the season. On the basis of these findings, it seems advisable to plant shells in Broad Creek during the first week of July.

Table 1. Percentage of animals setting on the upper- and under-plate surfaces, 1963–65. Plates were 4 inches apart in 1963 and 1 inch apart in 1964 and 1965.

Organism	1963		1964		1965	
	upper	under	upper	under	upper	under
Oyster	39.5	60.5	78.0	22.0	80.4	19.6
Barnacle	17.8	82.2	17.1	82.9	11.8	88.2
Flatworm	40.3	59.7	47.6	52.4	36.4	63.6
Bryozoan (2 species)	16.8	83.2	23.6	76.4	32.5	67.5
Mussel	45.3	54.7	89.2	10.8	85.8	14.2

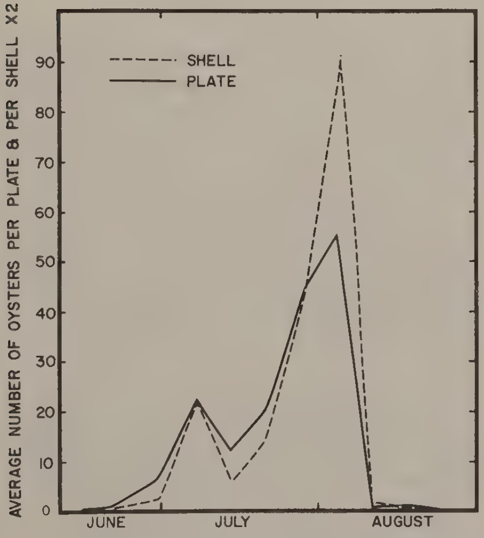

Fig. 9. Weekly fluctuations of oyster setting on asbestos plates and oyster shells for 1963 in Broad Creek.

Table 2. Preference (+) of several species of oysters for attachment to undersurface and upper surface.

Species	Surface		Reference
	Upper	Under	
Crassostrea virginica	+	+	Butler 1954[1]
Crassostrea virginica		+	Nelson 1927
Crassostrea virginica		+	Medcof 1955
Crassostrea virginica		+	Sieling 1950
C. gigas	+		Miyazaki 1938
" "	+		Yokota 1936
" "		+	Schaefer 1937
C. commercialis		+	Thomson 1950
Ostrea lurida		+	Hopkins 1935
O. edulis	+		Korringa 1940
" "		+	Cole and Knight-Jones 1939
" "		+	Knight-Jones 1951

[1] Butler reported that oyster spat were most numerous on the upper side of plates near the surface of the water, but on the lower side of plates near bottom.

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Volume 57 — June 1967

EFFECTS OF POLYSTREAM[1] AND DRILLEX[2] ON OYSTER SETTING IN CHESAPEAKE BAY AND CHINCOTEAGUE BAY

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ABSTRACT

The possibility of increasing the yield of oyster spat, Crassostrea virginica, *in Chesapeake Bay and Chincoteague Bay by treating shells with Polystream or Drillex was tested during 1963. Field studies were also conducted in Watts Bay, Virginia, to determine if the use of Drillex-treated sand in combination with Polystream-treated shells increased oyster setting.*

Significantly more oysters were caught on both Polystream-treated and Drillex-treated shells than on untreated shells when they were suspended either in the intertidal zone or placed on the bottom of Chincoteague Bay. Polystream-treated shells placed just off the bottom in the Tred Avon River, Chesapeake Bay, Maryland, also caught significantly more oysters than untreated shells. In Tangier Sound and Broad Creek in Chesapeake Bay, the difference in the amount of setting between chemically-treated and untreated shells was not significant.

Although in many cases more oysters were caught on chemically-treated shells, Polystream and Drillex apparently did not repel the principal fouling organism in Chincoteague and Chesapeake Bays.

In Watts Bay, setting was greater on plots with Polystream-treated shells and Drillex-treated sand than on either control plots (untreated shells only) or on plots with just Polystream-treated shells.

INTRODUCTION

In cooperation with the Bureau of Commercial Fisheries Biological Laboratory, Milford, Connecticut, the Biological Laboratory at Oxford, Maryland, initiated in 1963 the following studies: (1) measurement of the setting rates of oysters on cultch treated with Polystream or Drillex, and (2) evaluation of the use of Drillex-treated sand in combination with Polystream-treated shells as a method of increasing the yield of oyster spat.

Earlier experiments by the Milford Laboratory in Long Island Sound, Connecticut (Loosanoff, 1961a), indicated that shells dipped in Polystream (a mixture of chlorinated benzenes, of which 45 per cent is 1, 2, 3, 4-tetrachlorobenzene) had almost three times as many living spat as untreated shells, that spat were 20 to 25 per cent larger on treated shells than on undipped shells, that treated shells were much less fouled than untreated ones and that the number of drilled oysters on treated shells was only about one-eighth those on untreated shells. Loosanoff (1961b) also found that chemically-treated sand gave the oysters a considerable amount of protection from drill damage.

The purpose of this paper is to describe the re-

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[1] A polychlorobenzene product produced by Hooker Chemical Corp., Niagara Falls, New York. Polystream is a registered trademark. Mention of commercial products does not imply endorsement by the Bureau of Commercial Fisheries.

[2] An experimental compound containing 98 per cent Polystream and 2 per cent Sevin (a product of Union Carbide). Drillex is no longer manufactured.

[3] Present address: Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

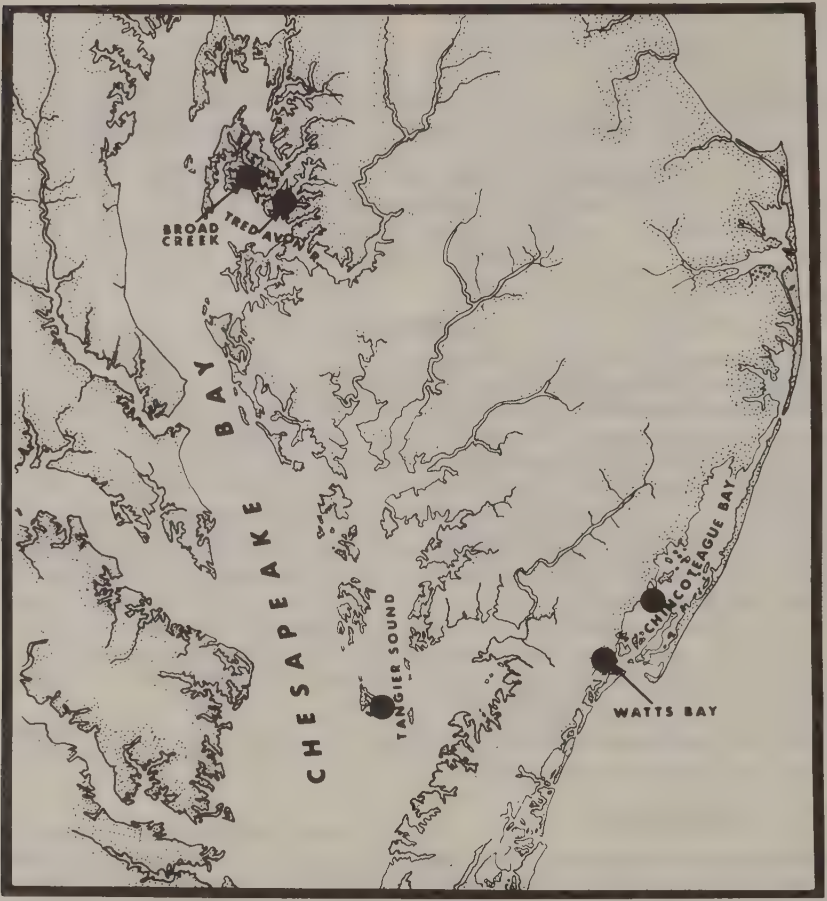

FIG. 1. *Location of stations, designated by solid black circles, in Chesapeake Bay, Chincoteague Bay, and Watts Bay where spat-collection studies were conducted.*

sults of a series of tests of shells, treated with Polystream and Drillex, to catch seed oysters and the results of attempts to increase oyster setting by using Polystream-treated shells in combination with Drillex-treated sand.

POLYSTREAM-AND DRILLEX-TREATED SHELLS AS CULTCH

Method

Following the procedure recommended by the Milford Laboratory (C. L. MacKenzie, Jr., Personal Communication), chicken-wire bags, each containing 24 clean, dry, oyster shells, were dipped into either Drillex or Polystream for 30 seconds and then allowed to drain for at least 2 to 3 hours. Chemically-treated and untreated shell bags were placed in four localities — three in Chesapeake Bay (Tangier Sound, Virginia, Tred Avon River and Broad Creek, Maryland) and one in Chincoteague Bay at Franklin City, Virginia (Fig. 1). The bags were left at all stations throughout the period of oyster setting.

Two ropes, each containing eight shell bags, 50 shells in each bag, were placed along the bottom (leased by a Virginia oyster grower) on the eastern side of Tangier Island. Each rope assembly had four bags of undipped control shells

TABLE 1. *Average number of spat on treated and untreated shells.*

Locality and treatment	Live spat per shell	Total spat per shell
Franklin City		
Intertidal — suspended		
Polystream	3.63	3.95
Drillex	2.48	2.75
Control	1.55	1.73
On bottom		
Polystream	0.20	0.57
Drillex	0.32	1.03
Control	0.04	0.25
Tangier Sound		
On bottom		
Polystream	0.63	1.91
Drillex	0.80	2.20
Control	0.48	1.66
Tred Avon River		
Off bottom		
Polystream	0.36	0.38
Drillex	0.20	0.21
Control	0.06	0.07
Broad Creek		
Off bottom		
Polystream	2.35	2.44
Drillex	2.47	2.59
Control	3.01	3.09

and four bags of chemically-treated shells — two dipped in Polystream and two in Drillex. These bags were in the water from 21 June to 25 September, 1963.

Six shell bags, two control and two dipped in each chemical, were suspended just off the bottom at four stations in Broad Creek and at five stations in the Tred Avon River. They were suspended on 13 and 14 June and retrieved on 30 and 31 October, 1963.

At Franklin City, 10 bags of shells treated with Drillex, 10 treated with Polystream, and 10 untreated bags were suspended in the intertidal zone, and a similar group were placed on the bottom. The bags at this station were in the water from 11 June to 14 October, 1963.

All shells at each locality were examined for the number of oysters, including live, drilled, boxes (dead oysters with both shell values still attached), and scars (only lower shell value present). In addition, all fouling organisms were counted either in per cent of shell covered, as with colonial calcarious bryozoans, or in actual number, as with barnacles. The shell heights (greatest dorsoventral distance) of all live spat were measured and their means compared statistically.

Setting on Shells

Oyster setting on the control and chemically-treated shells at each locality is shown in Table 1. In the intertidal zone of Chincoteague Bay, counts were 3.63 and 2.48 live spat per shell on those treated with Polystream and Drillex, respectively, as compared with 1.55 live spat per shell on undipped shells. The number of live spat on the Polystream-treated shells was significantly greater than on the control shells at the 5 per cent level; setting was also significantly greater on the Drillex-treated shells than on the control shells at the 5 per cent level. The difference between the setting on the Drillex-treated and Polystream-treated shells was not significant at the 5 per cent level.

Shells on the bottom in Chincoteague Bay caught considerably less spat than those in the intertidal zone. Shells treated with Drillex and Polystream had 0.32 and 0.20 live spat per shell

TABLE 2. *Average shell height of spat on treated and untreated shells.*

Locality and treatment	Mean height (mm)	Standard error of mean	Number
Franklin City			
Intertidal — suspended			
Polystream	35.5	0.33	879
Drillex	36.3	0.41	503
Control	34.9	0.53	375
On bottom			
Polystream	30.9	1.43	48
Drillex	26.3	1.00	75
Control	24.1	4.90	10
Tangier Sound			
On bottom			
Polystream	6.3	0.28	126
Drillex	6.6	0.32	156
Control	6.0	0.22	190
Tred Avon River			
Off bottom			
Polystream	33.5	1.15	47
Drillex	32.9	1.58	78
Control	33.0	2.88	14
Broad Creek			
Off bottom			
Polystream	30.9	0.50	447
Drillex	31.7	0.46	479
Control	32.5	0.39	573

whereas the control had 0.04 live spat per shell. The difference between the setting on chemically-treated and control shells was significant at the 5 per cent level. The difference between the two chemically-treated groups was also significant at the 5 per cent level.

Oyster setting in the Tred Avon River was light. Significantly more spat were caught on the Polystream-treated than on the control shells (at the 5 per cent level). The setting on the Drillex-treated shells and control shells did not differ significantly.

Untreated shells in Broad Creek had 3.01 live spat per shell compared with 2.35 and 2.47 per shell on the Polystream-and Drillex-treated shells, respectively. Differences among these were not significant at the 5 per cent level.

Setting was very light in Tangier Sound; numbers of live spat were only 0.63 and 0.80 per shell on shells treated with Polystream and Drillex respectively, and 0.48 on the untreated shells. As in Broad Creek, differences among the groups were not significant.

Degree of Fouling

At Franklin City, both the chemically-treated and untreated shells in the intertidal and bottom zones were heavily covered with fouling organisms. No differences were apparent between the two groups. Principal fouling forms were barnacles, calcareous tube worms and fleshy and calcareous bryozoans. MacKenzie, Loosanoff, and Gnewich (1961) found that Polystream was not effective against Bryozoa which are, unfortunately, among the principal fouling forms in Chincoteague Bay.

It is possible, since more spat were caught on chemically-treated shells, that both Polystream and Drillex inhibited or slowed down the growth of fouling organisms such as bryozoans when the shells were first placed in the water. This retardation would provide more clean surface for oysters to set. As the effects of the chemical become less, fouling would increase, and eventually reach a degree similar to that on the control shells. This hypothesis could be tested by examining chemically-treated and untreated shells weekly following their placement in the water.

TABLE 3. *Number of live oysters, scars, boxes, drilled boxes, and percentage of boxes drilled among shells placed on the bottom in Chincoteague Bay (see text for definition of scars and boxes).*

Shell treatment	Live spat	Total scars	Total boxes	Total set	Boxes drilled	
					number	percentage
Polystream	76	61	110	247	88	80
Drillex	48	41	48	137	39	81
Control (untreated)	10	36	15	61	13	87

It was difficult to evaluate the degree of prevention of fouling by the chemicals at Tangier Sound because of the accumulation of mud on the shells. Nevertheless, it appeared that the single-cell protozoan, *Folliculina* sp., was inhibited by Polystream and Drillex. Similar results for this species were found by MacKenzie, Loosanoff, and Gnewich (1961) in Long Island Sound.

In the Tred Avon River, difference in the degree of fouling between the chemically-treated and untreated shells was small, except for the number of barnacles. Setting of this species was 2½ to 3 times greater on the treated than on the control shells. In general, calcareous bryozoans were the principal fouling organism.

Chemically-treated shells placed in Broad Creek also caught 2½ to 3 times more barnacles than the control shells. As much as 50 per cent of the chemically-treated shells were covered with barnacles, which eliminated space on which oysters could attach.

Polystream and Drillex apparently do not repel the principal fouling organisms in Chincoteague Bay or Chesapeake Bay, i.e. barnacles, bryozoans, calcareous tube worms.

Growth of Spat

The shell height of all spat caught on both the chemically-treated and untreated shells was measured to the nearest millimeter. Mean heights at each locality of the oysters on treated or untreated shells were not significantly different (Table 2). The use of Polystream or Drillex neither improved nor hindered the shell growth of oysters.

Effectiveness of Chemicals in Repelling Oyster Drills

Among the shells placed on the bottom at Chincoteague Bay, 80 per cent of the boxes on Drillex-treated shells were drilled, whereas 81 and 87 per cent, respectively, of the total boxes on the Polystream-treated and control shells had been drilled (Table 3). It was not possible to determine if the scars had died from drill predation since the top shells were missing.

Several chemically-treated bags of shells in the intertidal zone fell to the bottom. One of them treated with Polystream had 17 drilled oysters and 48 live ones; a bag with Drillex-treated shells had 10 drilled oysters and 11 live spat. At Tangier Sound, as many oysters were killed by drills on the chemically-treated as on the control shells. It is apparent that the treatment of shells with Polystream or Drillex did not protect the spat from drill predation.

THE USE OF DRILLEX-TREATED SAND AND POLYSTREAM-TREATED SHELLS

Method

On 20 and 21 June 1963, three 1-acre plots, each measuring about 150 by 290 feet, were established on an intertidal seed oyster ground at Watts Bar in Watts Bay near Atlantic, Virginia. The distance between Plot I and II was 225 feet, whereas 750 feet separated Plot II from Plot III. Sixteen existing mounds of oyster shells, called rocks, were used on each plot. All rocks were covered with about 15 bushels of clean oyster shells, prior to the following treatment:

On Plot I, eight rocks received 15 bushels of shells dipped in Polystream and the other eight rocks were covered with an equal amount of untreated shells. Random ¼-square meter samples of the plot indicated an oyster drill population of 5.5 snails per square meter.

On Plot II, eight rocks received Polystream-treated cultch and the others were covered with undipped shells. On 28 June, 1963, after the shells were planted, 5 cubic yards of washed, kiln-dried sand previously mixed with 55 gallons of Drillex were spread over the plot. A drill population of 6.6 snails per square meter was found on this plot.

On Plot III (the control), each of 16 rocks received an additioned 15 bushels of untreated shells.

Treated shells were dipped in Polystream 30 seconds prior to being distributed on the rocks.

The washed, kiln-dried sand and 55 gallons of Drillex were mixed in a concrete-mixing truck. The sand was then loaded on a barge, carried to Plot II, and distributed evenly over the whole area. Observations were made periodically to determine the effects of the sand on the animals in the area. Beginning in November, ½-to 1-bushel samples of shells were collected from each rock to determine the intensity of setting. Poor weather conditions and unpredictable tides made it necessary to continue sampling throughout the winter so that all rocks could be examined. A spring spat count was made to evaluate winter kill, and a final count was made in early July to determine spat survival before the new 1964 wave of oyster setting.

Effects of chemicals on invertebrates and planted shells

Many invertebrates were found to be dying immediately after the application of the Drillex-treated sand. Animals that showed distress incuded two species of shrimp, *Crangon* sp. and *Palaemonetes* sp., mud crabs (Xanthidae) and polychaetes, *Scoloplos* sp. Fresh oyster boxes appeared several days after the sand had been applied, none of which were drilled. These mortalities appeared to stop 2 weeks after application; only an occasional box was found thereafter.

Shells treated with Polystream collected a layer of sticky silt. Though the silt on untreated shells could be rinsed away, it was necessary to rub it off the treated shells.

Setting

Routine examination of the shells within the experimental area from July through October indicated a poor set. The set was light also in other areas of Chincoteague Bay.

Spat counts on each plot are shown in Table 4. Highest counts of live spat per bushel were on Plot II where Drillex-treated sand was used. Setting was greatest on those rocks that received both Drillex-treated sand and Polystream-shells. Lowest counts were on the control Plot III.

Resampling of Plot II in July 1964 showed a higher number of oyster spat per bushel on the treated shells than when the plot was originally sampled. in December-January. Possibly some small spat were missed in the earlier examinations. Fluctuations in the number of spat on the untreated shells were considerable in Plot I. For example, counts in July 1964 from each rock on this plot ranged from 0 to 133 spat per bushel of shells. No counts on Plot I or Plot III, however, approached those on the rocks in Plot II where treated sand and shells were combined.

Plots I and II were resampled in July 1964 to study for drills and drill predation. Plot II had one drilled spat and no drills, Plot I yielded 20 drilled oysters and 9 drills.

DISCUSSION

The success of oyster setting always depends primarily on the availability of clean surfaces (Galtsoff, 1964). The fouling of shells prior to oyster setting is a serious problem in oyster management. To reduce fouling, states attempt to time their plantings of shells as close as possible to the initiation of the setting season. This procedure is sometimes impossible when large quantities of shell must be distributed over a wide area. Shells planted too early become fouled and are inefficient as spat collectors.

One answer to the problem of early planting of cultch is treatment of shells with an anti-fouling chemical. Thus the shells, though in the water several months before oyster setting begins, are still clean. Some success in reducing fouling has been made in Long Island Sound by the use of Polystream (MacKenzie, Loosanoff, and Gnewich, 1961).

The biota differs in each geographic location; though chemically-treated shell may inhibit the

TABLE 4. *Average counts of spat per bushel of shells on experimental plots.*

Plot	Months of Sampling	Live spat per bushel on Untreated shells	Live spat per bushel on Treated shells
I	Nov. 1963	51.4	164.8
II	Dec.-Jan., 63-64	260.9	299.6
III	Mar. 64	13.1	—
I	Mar. 64	29.3[1]	—
I	July 64	92.7	74.7
II	July 64	255.3	586.0

[1] Sampled for winter kill,

setting of fouling organisms in one area, the same results may not be obtained at another location with a completely different group of animals. The results of our study offer an example of the importance of these local differences for in Chesapeake and Chincoteague Bays, the principal fouling organisms apparently were not repelled by Polystream or Drillex.

In Long Island Sound the setting of the barnacle, *Balanus balanoides,* was reduced considerably when shells were treated with Polystream; treated shells had only one-seventh as many barnacles as untreated controls (MacKenzie, Loosanoff, and Gnewich, 1961). In Broad Creek, Chesapeake Bay, the setting of a different species of barnacle, *Balanus improvisus,* was 2½ to 3 times heavier on chemically-treated shells than on untreated shells. Preliminary tests obviously should be made at each new location before commercial application is attempted.

Over seven times more spat were caught in this study on plots with Polystream-treated shells and Drillex-treated sand than on plots that had only Polystream-treated shells. Setting in Chincoteague Bay during the test year (1963) unfortunately was light. But, because of significant differences in setting between the chemically-treated and untreated plots, we believe further investigation on commercial use of chemical treatments should be made. Since Drillex is no longer manufactured, Polystream-treated sand could be substituted.

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Postscript

While this manuscript was in press, a paper entitled: "Effects of the Treatment of an Oyster Bed with Polystream and Sevin" by Dexter Haven, Michael Castagna, Paul Chanley, Marvin Wass, and James Whitcomb appeared in the December, 1966 issue of *Chesapeake Science,* 7(4):179-188. The authors reported that Polystream-Sevin did not control drills on treated plots at Hog Island Bay, Virginia, and oyster production was not increased by treatment. As in our study, the addition of the chemically-treated sand initially killed the invertebrates in the area.

Freeze-Drying for Determining Total Solids in Shellfish

A customary method of measuring the condition of shellfish is determination of percentage of solids (Engle, 1950, 1958; Shaw, 1961). The formula for determining solids content is simple — dry weight of meat (grams) divided by the wet weight of meat (grams) times 100. Since 1965 this laboratory has been following the seasonal changes in the percentage of solids in the Atlantic surf clam, *Spisula solidissima*, and the American oyster, *Crassostrea virginica*. Monthly samples have been analyzed to determine when shellfish are in their best condition and will yield the greatest volume of meat.

The conventional method of determining percentage of solids is by the oven-dry technique (Engle, 1950). At our laborarory, after we obtain the wet weight of meat, the sample is oven-dried for 24 hr at 50 C and 24 hr at 90 C. Westley (1961) oven-dried oysters 2 days at 50 C and 2 days at 100 C. Disadvantages of this method are the time necessary to dry meats (at least 48 hr) and the unpleasant odors given off by the drying meats. After oven-drying, meats must be cooled in a desiccator before weighing because they are extremely hygroscopic.

The principal source of inconsistency is the treatment of oyster meats before determination of their wet weight (Galtsoff, 1964). To eliminate error, we pry oysters open at the hinge and shake out the free fluid. The adductor muscle is then cut and the meat and remaining liquor are placed in an evaporating dish. Galtsoff (1964) stated, "This method gives a lower percent of solid than those obtained with other procedures (e.g., draining meats before weighing) because bleeding is minimized."

This report describes the freeze-dry technique, compares it with the oven-dry method, and reports and evaluates other methods of measuring shellfish condition.

Procedure.—A Thermovac freeze-dryer, Thermovac Industries Corp., Copiague, New York, Model FD-1, was used to process all animals. Two accessories were obtained for bulk drying — a lucite vacuum drum, 20 inches high and 12 inches in diameter, and a 3-tray heat rack, 19 inches high and 9 inches in diameter.

The procedure was as follows:

Oysters

1. Wash oyster to remove mud and excess fouling.
2. Open oyster at the hinge, taking care not to puncture the meat or cut the adductor muscle.
3. Shake to drain shell-cavity fluids.
4. Cut adductor muscle, and place oyster and fluids into a pre-weighed evaporating dish; weigh dish and meat to nearest centigram.
5. Place dish in freezer until meats are solidly frozen.
6. Transfer frozen oysters to freeze-dryer drum and process 12 hr.
7. Immediately weigh to nearest centigram.

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For composite analysis, follow steps 1–3, then place desired number of oysters in blender and grind at high speed for 2 min. Place about 20 g of blended meats into an evaporating dish and weigh. Follow steps 5–7. As many as 20 samples can be processed during a single run.

Surf clams

The procedure for determining percentage of solids of surf clams is similar to that for oysters except it is necessary to shuck and then wash and blend the meats. All sand should be removed before freezing the samples. After freezing follow steps 6 and 7 for oysters.

Calculations

$$\text{Per cent solids} = \frac{\text{dry weight of meat} \times 100}{\text{wet weight of meat}}$$

Comparison.—A comparison of duplicate samples processed by the freeze-dry and oven-dry techniques was made for oysters and clams. As shown in Fig. 1, the difference between oyster samples was consistent; the percentage of solids for freeze-dried oysters was slightly higher in every comparison and the average difference was 0.3. Though the results for surf clams were not as consistent as for oysters (Fig. 2), the average difference between the oven-dry and freeze-dry methods was 0.3, similar to that found for oysters.

The fact that the percentage of solids for oven-dry oysters was lower indicated either that volatile substances other than water were being removed by oven-drying or that a small quantity of water was retained in the freeze-dried meats.

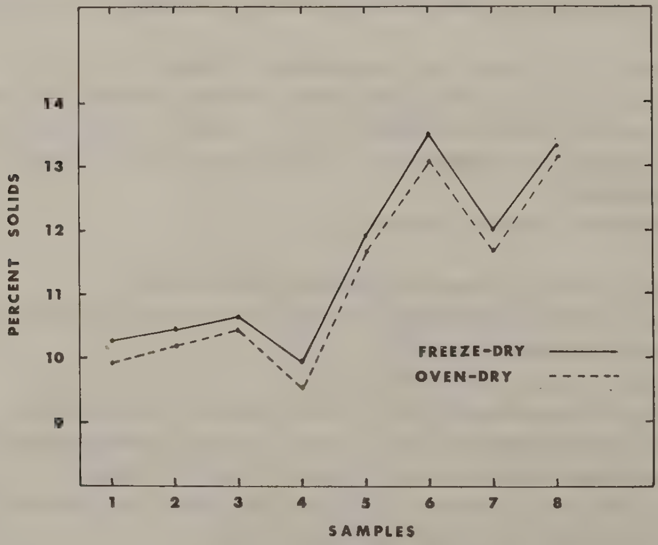

FIG. 1. The percentage of solids for eight duplicate samples of oysters determined by the freeze- and oven-dry methods.

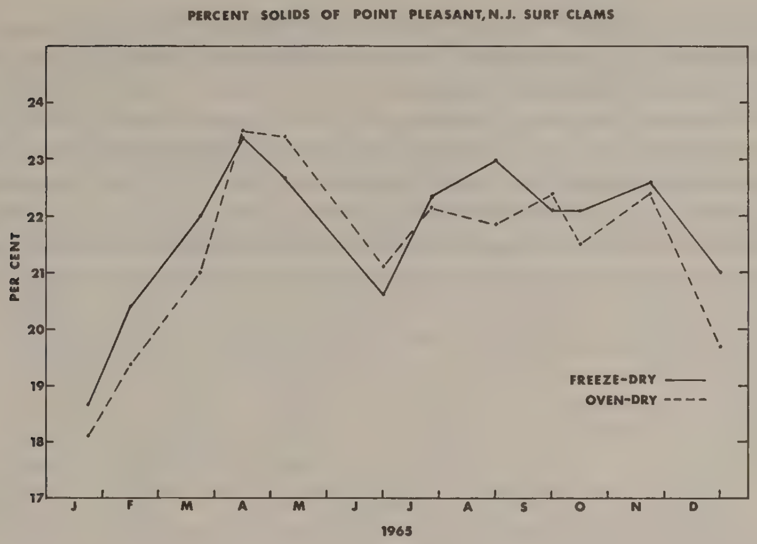

FIG. 2. The percentage of solids for 12 duplicate samples of surf clams taken monthly during 1965, determined by the freeze- and oven-dry methods.

Other methods.—Many methods have been used to determine the quality of shellfish meat. The simplest procedure (and probably the one most subject to errors) is by visual inspection. Oysters are opened and the meats rated from 1 to 10; a rating of 1 indicating an extremely poor or watery oyster, and a rating of 10 an extremely "fat" oyster. This method, though highly subjective, is commonly used during field surveys when other techniques are not practical.

Another simple method of measuring meat quality is to shuck a given number of oysters and record the volume displacement. This technique gives a commercial estimation of the yield from a bushel of oysters.

Laboratories generally use more refined methods to obtain an estimate of meat quality. First, and probably the most common procedure, is a determination of the index of condition (CI), originally devised by Grave (1912) and later modified by Higgins (1938). The index of condition is calculated by dividing the dry weight of the meat (grams) times 100 by the volume of the shell cavity (milliliters); some investigators, as Medcof and Needler (1941), use a multiplier of 1000. This method has several disadvantages: (1) the oyster must be carefully cleaned of all fouling organisms and mud; (2) the total volume of oyster and shell alone must be measured by volume displacement (difference between the two equals the volume of the shell cavity); and (3) the meats must be oven-dried to a constant weight 48 hr. Both Korringa (1955) and Carver (1966) eliminated oven-drying by measuring water content through toluene distillation. Although Carver's method required about 45 min to process meats, only one sample could be run with his apparatus.

Several modified indexes of condition have been proposed. These include meat volume divided by shell-cavity volume times 100 (Baird, 1957) and wet weight of meat divided by volume of shell cavity times 100 (Chew et al., 1965). Both techniques require the slow process of measuring cavity volume. In the latter method serious errors can occur.

A comparison was made between the percentage of solids, index of condition (dry weight of meat), and modified index of condition (wet weight of meat) on 50 oysters processed monthly (Shaw, 1961) (Fig. 3). The percentage of solids and index of condition followed similar seasonal changes. But, when these two methods were compared with the modified index of condition, several discrepancies were apparent. In October 1959, the condition of oysters rose when measured by the first two methods, but the modified index showed a decline in oyster condition. The second discrepancy, and by far the most serious, was the drop in condition during the spawning season. Though correctly shown by the percentage of solids and index of condition as a decline in June–July, the modified index showed a rise in condition during this period. Finally, what seemed to be significant changes in oyster condition as measured by percentage of solids and index of condition, appeared as slight changes when analyzed with the modified index (Fig. 3). On the basis of these comparisons the use of wet weight of meats instead of dry weight can give a false condition factor.

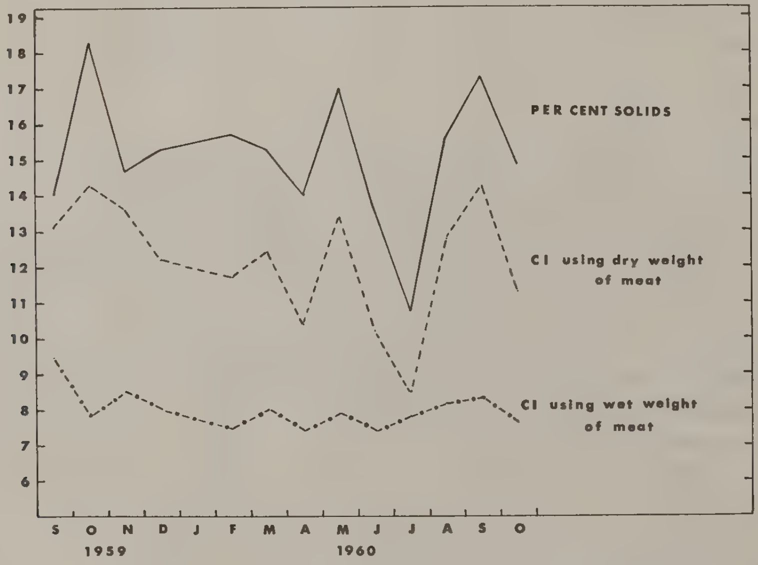

FIG. 3. The percentage of solids, index of condition, and modified index of condition of oysters sampled monthly in 1959 and 1960 from Taylors Pond, Chatham, Massachusetts. Left-hand scale refers to both percentage of solids and condition index units.

The most precise measure of quality is determination of glycogen content of oyster tissue (Calderwood and Armstrong, 1941; Engle, 1950). The higher the glycogen content the "fatter" is the oyster. This method requires meticulous preparation of the sample and of chemical solutions. When accurate knowledge of the true "fatness" of shellfish meats is essential, however, glycogen content should be measured.

Conclusions.—Except for index of condition, the percentage of solids is probably the most common laboratory method of measuring the condition of shellfish meats. The two methods yield similar seasonal trends, but percentage of solids is easier to measure. Determination of solids is further refined when the freeze-dry technique is used. Processing time is reduced from 48 to 12 hr, unpleasant odors are eliminated, and meats can be weighed immediately after freeze-drying because they are at room temperature. Also, using a 3-tray rack, 20 samples can be processed at one time. The freeze-drying equipment may be more expensive, but the time saved and ease of processing by freeze-drying cancels the initial extra cost.

Because of the speed, accuracy, and convenience, it is recommended that the freeze-dry method be adopted as a standard laboratory procedure for determining the percentage of solids of shellfish meats.

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Coastal Zooplankton

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This article contains an excellent list of references and an outline which is a valuable help to teachers and students who are interested in collecting and examining zooplankton.

Introduction

The zooplankton demonstration outlined here is designed to give students the opportunity to collect and examine zooplankton and to discuss certain aspects of zooplankton biology. Collections can be made from nearshore coastal waters, the surf zone, or tide pools. Students are given the opportunity to examine the myriad of small animal forms which constitute zooplankton. They are provided with the opportunity to discuss variation in body structures among the different forms, including the intricate structure of appendages modified for use in swimming, feeding, respiration, and reproduction. Collections of zooplankters can be made before the class period. It is suggested, however, that two sessions be given to the lesson, the first incorporating a collecting trip, second, laboratory examination and discussion.

Zooplankton is a term applied to a vast group of small, passively floating organisms which serve as an important link in the food chain of the ocean. They are grazers on the expansive pastures of phytoplankton, the minute unicellular plants which are the basic synthesizers of carbohydrates, fats, and proteins in the sea. The oceanic food chain, basic to the natural economy of the sea, can be expressed as a pyramid of numbers with the smaller more prolific phytoplanktonic synthesizers at the base, and the numbers of the progressively larger, less fecund, predators decreasing toward the apex (Fig. 1). Zooplankters convert and concentrate the minute phytoplankters into animal substance large enough to be utilized by the larger marine organisms, most of which are incapable of feeding directly on small phytoplankters.

Zooplankters occupy a variety of niches and reflect sharply environmental differences in salinity, temperature, light, density, water circulation, and other physical factors. The large-scale horizontal movement of these small animals is dependent on ocean currents which makes them useful indicators of hydrographic conditions.

Composition of coastal zooplankton varies with local hydrographic conditions. Although species composition may vary with area and season of collection, the 21 animal groups listed in Table 1 are likely to be present in most coastal tow-net collections. Several members of the coastal zooplankton community of the Gulf of Maine are shown

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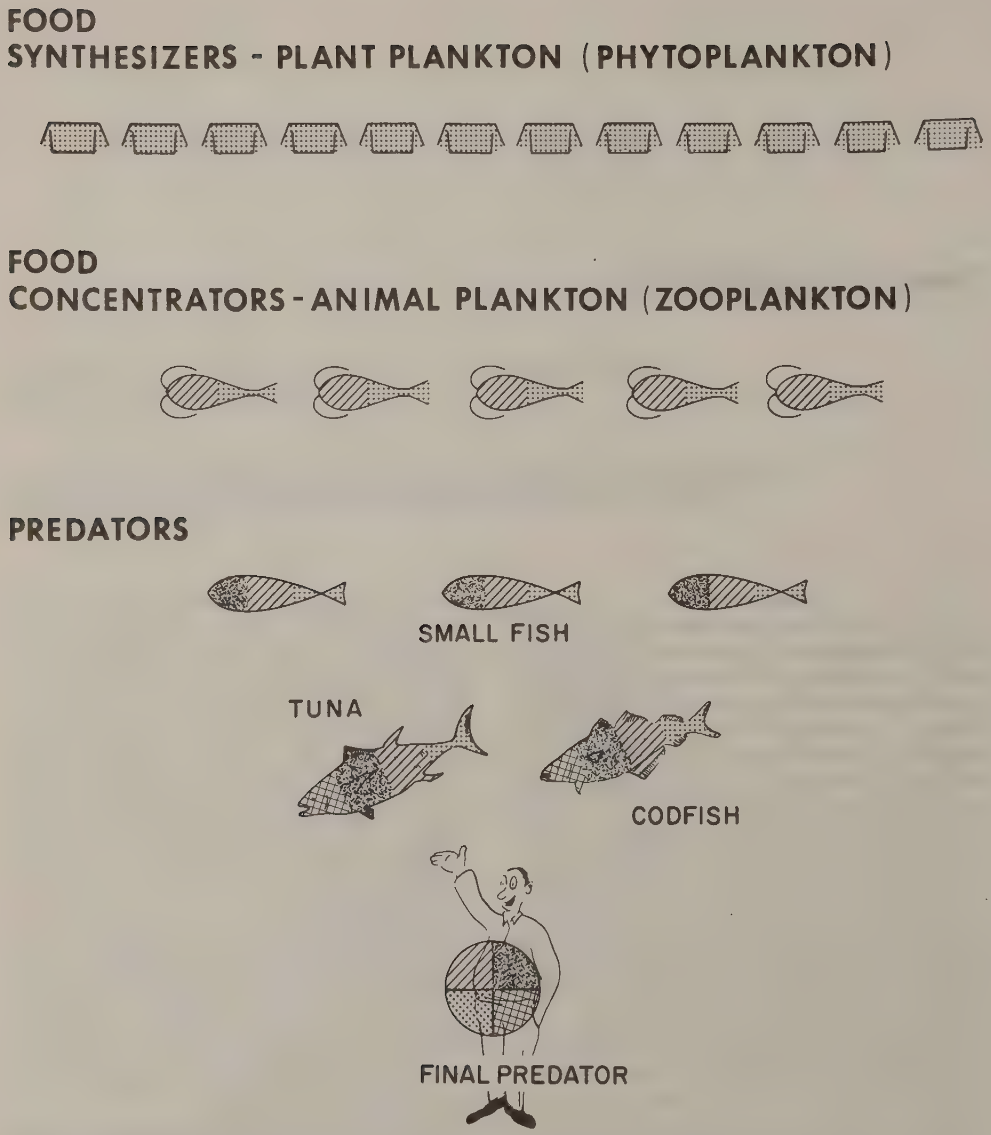
FOOD
SYNTHESIZERS - PLANT PLANKTON (PHYTOPLANKTON)
FOOD
CONCENTRATORS - ANIMAL PLANKTON (ZOOPLANKTON)
PREDATORS
SMALL FISH
TUNA
CODFISH
FINAL PREDATOR

Fig. 1. Schematic representation of the oceanic food chain. Depicted at the top is the food chain base and at the bottom, the apex.

in Fig. 2. Of the seven groups shown, copepods are the dominant forms. They generally constitute from 40 to 85% of the total zooplankton in the upper 20 meters of coastal water.

Demonstration

Students have shown great interest in examining tow-net collections of zooplankton to determine major groups, and even species composition of the catch. Several excellent taxonomic source books to facilitate identifications to major groups are available. They are listed in the References section. Species identification is not suggested, since it is a most difficult task requiring detailed study of morphological characteristics. It is possible, however, for the instructor to prepare diagnostic keys for student use if species identification is attempted. Taxonomic specialists in the scientific community can be contacted for pertinent reference materials (see Blackwelder, 1961). Students observing either living or freshly preserved zooplankton for the first time will be astounded by the variety of shapes, brilliance of body coloration, and elaborate forms of the appendages modified for feeding, swimming, and reproduction. Attention can be focused on the relations between body form and adaptation to planktonic existence in the marine environment.

A lively discussion regarding structural adaptation for survival in the marine environment could result from microscopic observations of geniculate antennae of copepods, compound eyes of amphipods, plumose flotation appendages of nauplii, and a myriad of other structures. For example, the fine network of setae on the maxillae of copepods, used for filtering phytoplankton, can be observed under high power of a standard

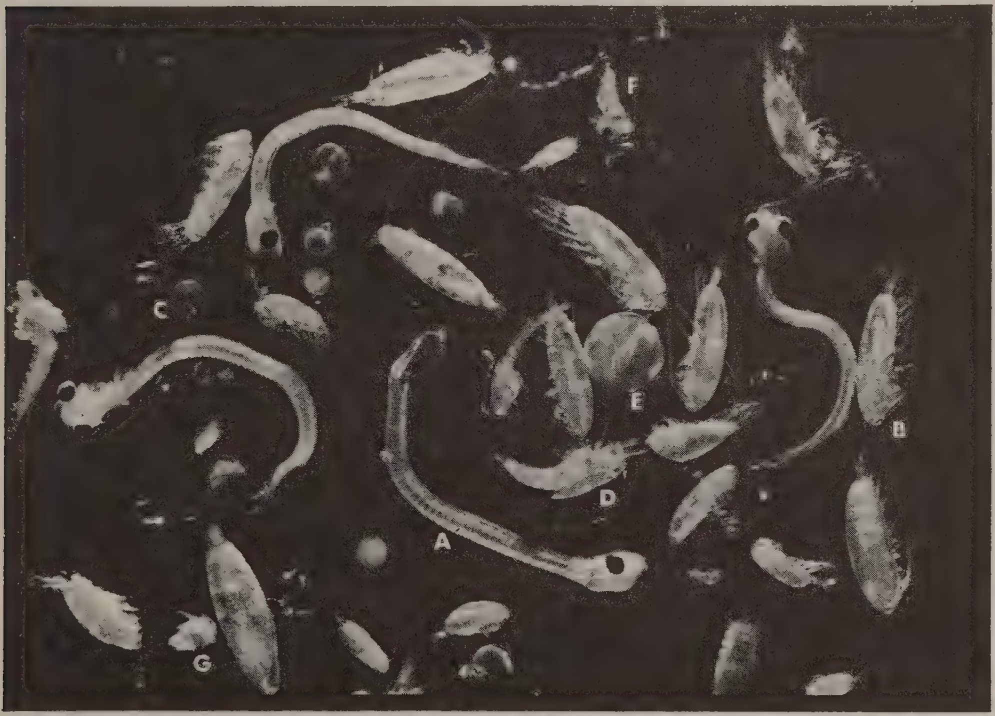

Fig. 2. Members of the Gulf of Maine coastal zooplankton community. The large-scale horizontal distribution of these small animals is dependent on oceanic currents, which makes them useful indicators of hydrographic conditions. Zooplankters shown are: (A) herring larvae, (B) copepods, (C) pelagic mollusks, (D) decapod larvae, (E) fish egg, (F) Cladocera, and (G) barnacle nauplius.

monocular laboratory microscope. For rapid examination the entire copepod can be stained in a solution of lactic acid and methyl blue prior to dissection of the maxilla. Lactic acid serves as a suitable temporary mounting medium. The maxilla should be placed in a drop of lactic acid on a glass slide. Careful addition of a cover slip provides a temporary slide mount suitable for microscopic examination. Appendages of other crustaceans also can be observed in this manner.

Materials and Methods

Zooplankton can be collected in a variety of ways, ranging from elaborate devices for continuous net sampling from a boat underway to a small net cast from shore and hauled in by hand. Nets can be fished from bridges, or scoops can be made into a tide pool with a fine-mesh juice strainer, and contents emptied into a gallon jar. Formalin preservative can be added in the field (5% solution), or the container of living zooplankton can be kept overnight. The temperature should be cool (approximately 50° F) and the organisms uncrowded (approximately 100 per quart).

Laboratory apparatus

Useful laboratory apparatus for examination of zooplankton includes:

1. Assorted glass beakers (25, 50, 100 mls)
2. Syracuse dishes
3. Petri dishes: used for sorting zooplankters under the microscope. The dish should be marked off into 1 cm divisions for ease in examining samples.
4. Small (4-dram) vials for storing separated specimens.
5. Binocular dissecting microscope (10X, 15X, 20X).
6. Sample divider. Usually the sample will contain far too many organisms for efficient examination. Divide the sample into aliquots, or stir well and remove a representative subsample with a pipette.

Before the subsample is taken for identification, students may be paired—one to record, the other to identify for alternating periods of time. The animated discussions between the two team members regarding

Fig. 3. Suggested Data Sheet Format

DATE: ______________ DATA SHEET NO. ______________

ZOOPLANKTON COUNT

Location ______________ Station ______________ Sample ______________
Date ______________ Salinity ______________ Amount of water strained ______________
Position ______________ Temperature ______________ Time of Tow: In: ________ Out: ________
Fraction of sample examined ______________ Examined by: ______________

Species	Number		No./100m^3	Sex	Remarks
	Aliquot	Total			
1.					
2.					
3.					
17.					
18.					

Table 1. Animal Groups Expected in Most Coastal Tow-Net Collections

1. Medusae
2. Ctenophora
3. Siphonophora
4. Chaetognatha
5. Annelida
6. Copepoda
7. Cladocera
8. Ostracoda
9. Euphausiacea
10. Amphipoda
11. Mysidacea
12. Decapoda
13. Pteropoda
14. Tunicata
15. Fish eggs and larvae
16. Gastropod larvae (veliger)
17. Pelecypod larvae (veliger)
18. Echinoderm larvae (pluteus)
19. Brachyura larvae (zoea)
20. Cirriped larvae (cypris)
21. Other crustacean larvae (nauplii)

possible identification sharpens individual observational prowess. Taxonomic descriptions of major zooplankton groups should be readily available during the laboratory session. A number of the papers listed under taxonomic references can be obtained on loan from university libraries. For general background material Miner (1950) is most useful. Data sheets should be provided for recording and tabulating the identifications (Fig. 3).

Expected Results

Individual counts of zooplankton groups present can be made by students, from which percentage composition of various zooplankters can be determined. If the amount of water strained to obtain the original sample is known, the total numbers present per unit of water strained can be determined.

If zooplankton samples are collected from several different coastal areas, comparisons of species composition can be made and possible reasons for different results discussed—particularly if environmental observations are made during the collecting trip, on condition of tide, water temperature, salinity, transparency, direction and velocity of the current, meteorological conditions, and other measurable physical factors of interest.

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A REDESCRIPTION OF THE CALANOID COPEPOD, *PONTELLA VALIDA* DANA, FROM THE CENTRAL SOUTH PACIFIC

BY

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INTRODUCTION

A new species of pontellid copepod designated as *Pontella valida* was described by Dana (1852). The description was limited to a male specimen of "abnormal form" collected from the area "north of New Zealand toward Tongatabu". Two samples collected from this area during cruise 55 of the U. S. Bureau of Commercial Fisheries research vessel "Charles H. Gilbert" (January to March 1962) contained male specimens similar to Dana's in the bilobed structure at the distal end of the right fifth leg (Dana, 1852: pl. 82 fig. 6) and females similar in abdominal and furcal structure to a so-called "bizarre" form of *Pontella tenuiremis* figured by Wilson (1950: pl. 17 fig. 216). Although my specimens differ from Dana's in the structure of the right antenna (lacking the broadly developed spine on the anterior margin of the seventh segment, and in the bilobed pedestal structure on the tenth segment), and in the segmentation and structure of the abdomen, the similarity in type locality and in the structure of the male right leg suggests that the normal form of Dana's specimen, if available, would be identical to my specimens. The discrepancies in form of the antennae are likely attributable to the poor optical equipment available to Dana. Unfortunately, Dana's type material was apparently lost in the wreck of the vessel "Peacock" on its return voyage to the United States, and is not in the U. S. National Museum Collection (T. E. Bowman, personal communication). Wilson (1950: 301) has given the only existing reference to *P. valida* following Dana's description. However, his description and figures (figs. 432-443) are incorrectly attributed to *P. valida*; rather than this species, they represent *Pontella elephas* (Brady), recently redescribed by Wickstead & Krishnaswamy (1964) as *Ivellopsis elephas*.

Copepods collected during the "Albatross" Eastern Pacific cruise (1904-1905), identified as *P. tenuiremis* by Sars and Wilson, were kindly made available for examination by Dr. Thomas E. Bowman of the U. S. National Museum. Of 119 specimens examined, 27 (13 males, 14 females) were identical to the *P. valida* form found during "Charles H. Gilbert" cruise 55. These specimens differ significantly from previously published descriptions of *P. tenuiremis* by Giesbrecht (1892), Wilson (1942, 1950), and Grice (1961), particularly in the bilobed structure at the distal end of the right fifth leg, and in the thumb-like protuberance on the right margin of the female urosome. A redescription of *Pontella valida* is given here, with observations on hydrographic conditions in the sampling area.

Pontella valida Dana (figs. 1-23)

Localities and materials. — Surface tows from the U. S. Bureau of Commercial Fisheries research vessel "Charles H. Gilbert" cruise 55, January to March 1962: 24° 01′ S 171° 43′ W, Station 43, Feb. 11, surface temperature 26.2° C, surface salinity 35.15‰, 5 males, 4 females — 20° 52′ S 173° 28′ W, Station 92, March 10, surface temperature 27.2° C, surface salinity 35.34‰, 2 males, 1 female. Deposited in the Invertebrate Collection, U. S. Bureau of Commercial Fisheries Biological Laboratory, West Boothbay Harbor, Maine.

Measurements. — Total length was measured from the anterior margin of the head to the distal margin of the furca; the cephalothorax from anterior margin of the head to posterior margin of the last thoracic segment, along the midline plane; and length of abdomen from the anterior margin of the genital segment to the distal end of the longest ramus. Total lengths and cephalothorax-abdomen ratios of undamaged specimens are given in table I.

Description. — Female (figs. 1-17). In dorsal view, lateral margins of head produced into symmetrical side hooks. Thorax 5-segmented, with posterior corners of the fifth segment ending in symmetrical angular processes (fig. 1). Lateral view shows well developed rostrum and large lens facing rostral base (fig. 2). The rostrum is bifid and symmetrically acuminate with no visible lens structure (fig. 3). Posterior margin of fifth thoracic segment ends in an acute angular process (fig. 2).

Abdomen 2-segmented, asymmetrical in dorsal view, with a large thumb-like protuberance on right margin. Left margin smoothly curved, terminating with angular indentation at furcal base (fig. 4). Genital opening situated medially in ventral view (fig. 5). In lateral view thumb-like protuberance on right side is directed posteriodorsad (fig. 6). Furca asymmetrical, right branch wider and more angular than left (fig. 4).

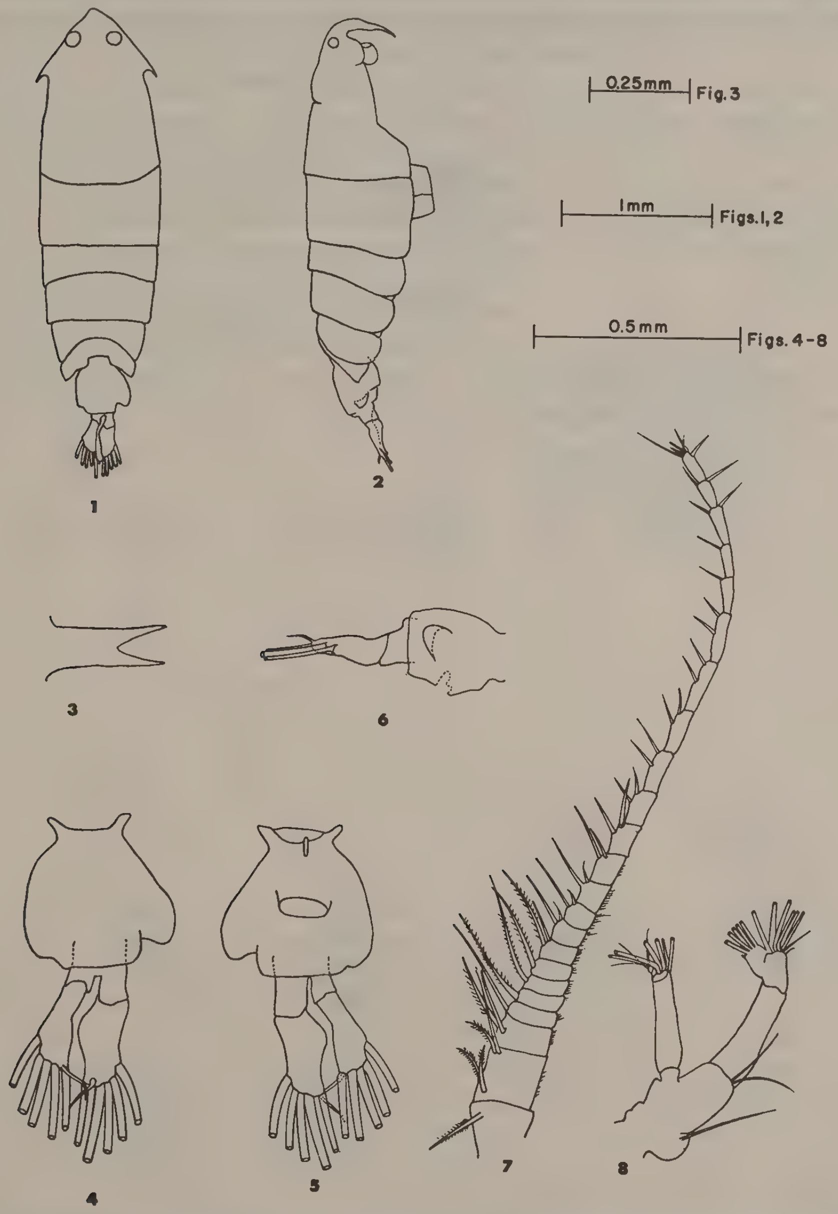
First antennae symmetrical, reaching approximately to posterior quarter of third thoracic segment. Antennae (fig. 7) with 23 distinct segments, all with spines on the anterior margin. Segments 2 to 12 bear small setae on posterior margins. Single spines on posterior margin of segments 21 to 23. Segment 23 bears 4 spines on the distal margin.

Second antenna with 4-segmented exopod and 2-segmented endopod. Distal segments of exopod have 6 large and 3 small setae. Endopod bearing 6 setae on the distal lobe, 6 large setae, 1 medium-length seta, and 1 small seta on proximal lobe (fig. 8).

Mandibular gnathal lobe has 8 teeth, with 2 ventralmost monocuspate, adjacent 3 bicuspate, and dorsal 3 monocuspate (fig. 9).

First maxilla with 13 setae on gnathobase, 3 on inner lobe of lacinia, and 4 on outer lobe. Exopod weakly separated from basipodite, bearing 10 large setae and a single slender seta; 5 setae originate from single base on distal margin of endopod (fig. 10).

Second maxilla with 8 well-developed and 5 slender setae on first basipodal


0.25mm Fig. 3
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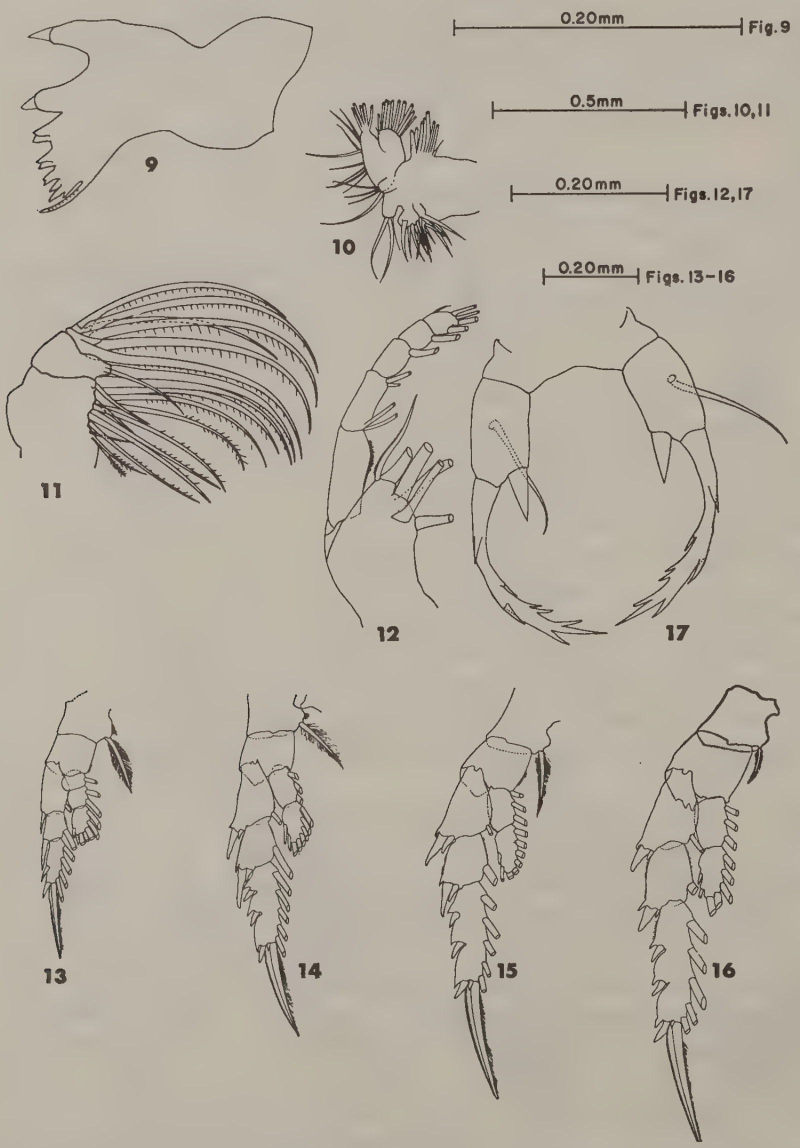
1
2
3
6
4
5
7
8

Figs. 1-8. *Pontella valida* Dana, female. 1, dorsal view; 2, lateral view; 3, rostrum; 4, abdomen, dorsal view; 5, abdomen, ventral view; 6, abdomen, lateral view; 7, first antenna; 8, second antenna.

segment, 1 large and 1 small seta on second basipodal segment. Anterior terminal margin with 5 large setae, and single small seta (fig. 11).

First basal segment of maxilliped strongly developed, bearing 5 large setae and single smaller seta with denticulate outer margin. Inner margin of the second segment armed with small spiniform denticles. Paired setae positioned at junctions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Figs. 9-17. *Pontella valida* Dana, female. 9, mandibular gnathal lobe; 10, first maxilla; 11, second maxilla; 12, maxilliped; 13, first leg; 14, second leg; 15, third leg; 16, fourth leg; 17, fifth legs.

of segments 2 and 3 and 3 and 4. Single seta fixed to anterodistal corners of segments 4, 5, and 6. Three setae rise from anterior margin of the distal segment, and a small seta from the outer margin (fig. 12).

First pair of swimming legs with 3-segmented endopods and exopods (fig. 13). Swimming legs 2, 3, and 4 with 3-segmented exopods and 2-segmented endopods (figs. 14-16). All legs bear denticulated terminal spines.

Fifth legs 3-segmented and symmetrical, with single long seta positioned medially on second segment. Endopod spiniform, exopod bearing 8 spiniform processes, 4 on inner margin, 3 on outer margin, and 1 at apex (fig. 17).

Male (figs. 18-23). Lateral margins of head with symmetrical side hooks. Thorax 5-segmented, with posterior margins of fifth segment slightly angular (fig. 18). In lateral view rostrum well developed with large lens facing rostral base (fig. 19). Rostrum bifid, symmetrically acuminate, and as in female, with no distinguishable lens structure (fig. 20).

Abdomen 5-segmented, with moderately developed lateral process on left margin of genital segment. Furca symmetrical, approximately 3 times longer than wide (fig. 18). Total length and cephalothorax-abdomen ratios are given in table I.

TABLE I

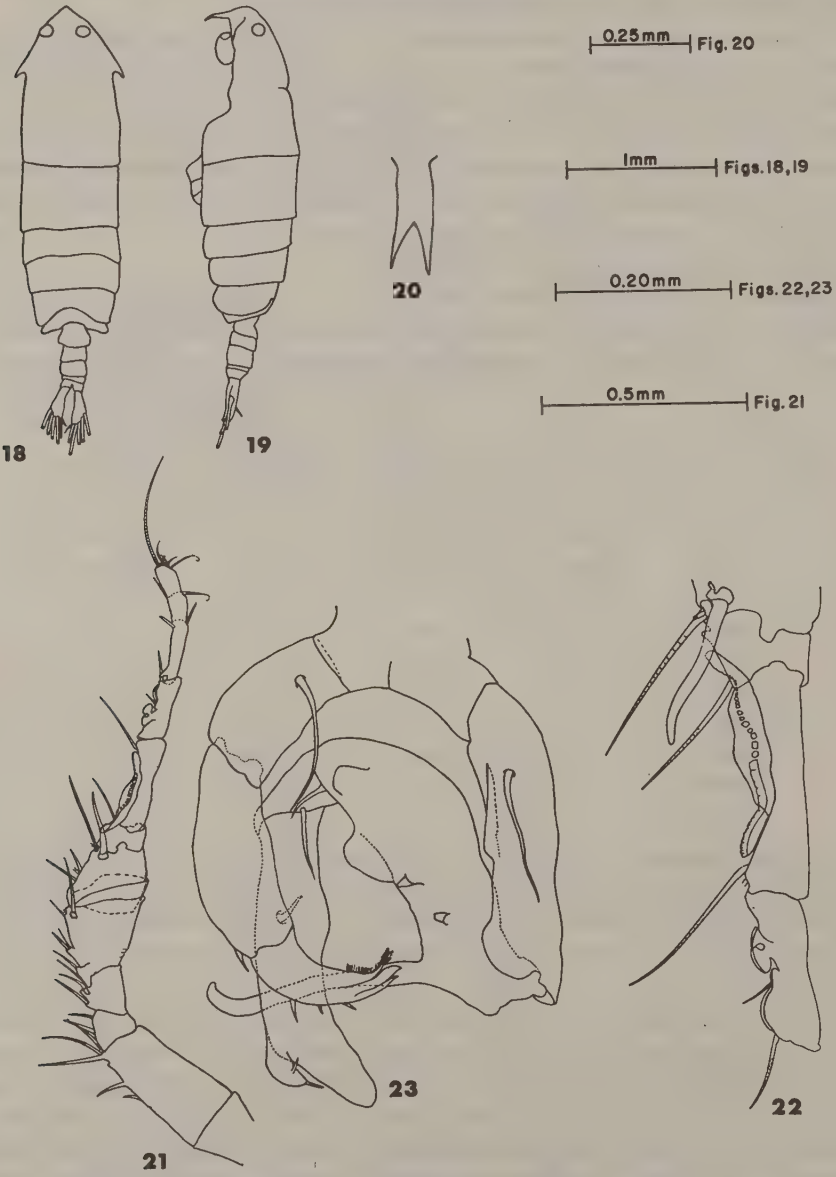
Measurements of *Pontella valida* Dana, "Charles H. Gilbert" cruise 55

Station	Sex	Total length mm	Cephalothorax length mm	Abdomen length mm	Cephalothorax-abdomen ratio
92	Male	2.57	1.94	0.63	3.1 : 1
	Male	2.57	1.94	0.63	3.1 : 1
	Female	2.45	1.88	0.57	3.3 : 1
43	Male	2.74	2.06	0.68	3.0 : 1
	Male	2.57	1.94	0.63	3.1 : 1
	Female	3.03	2.34	0.69	3.4 : 1

Geniculate antenna with 11 distinguishable segments (fig. 21). Distal segment developed into three non-articulating divisions, suggestive of secondary fusion. Segment 7 armed with broad spine. Segment 9 bears ridge of lamellate denticles. Sigmoid ridge and bilobed pedestal, both with lamellate denticles, on segment 10 (fig. 22).

Male fifth legs (fig. 23) bear single seta on medial plane of second segment. Right leg with sloping ridged process on the inner margin of the second segment. Cheliped of right leg massive, bearing elongated thumb, 2 small denticles, large ridgelike process and 2 well developed spines on inner margin. Distal margin of terminal segment ends in 2 asymmetrical lobes, smaller lobe bearing 2 small spines, 1 medial and 1 distal. Penultimate segment of left leg armed with single spine at anterior outer margin. Distal segment bears 3 short spines on outer anterior margin, and 3 lamelliform processes at the distal end with medial process well developed and inner process bearing small setae (fig. 23).

Remarks. — *Pontella valida* is similar to *Pontella tenuiremis* Giesbrecht, but can be distinguished by the bilobed structure of the distal end of the male right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0.20mm Figs. 22, 23
0.5mm Fig. 21
18
19
20
21
22
23

Figs. 18-23. *Pontella valida* Dana, male. 18, dorsal view; 19, lateral view; 20, rostrum; 21, right first antenna; 22, segments 6 to 9, right first antenna; 23, fifth legs.

fifth leg and absence of any elongate process at the proximal end of the thumb. In the female the distinguishing characters are the asymmetrical abdomen bearing a large thumb-like protrusion on the right margin, the angular indentation at the furcal base on the left abdominal margin, the asymmetrical furca, and the fifth feet in which the endopod is spiniform and the exopod bears 8 spiniform processes.

Hydrographic observations. — During "Charles H. Gilbert" cruise 55, 60 surface plankton tows were taken in waters between latitudes 20° N to 25° S, and longitudes 165° E to 155° W. The surface temperature ranged from 23.8° C in the northern region to 29.5° C in the vicinity of Samoa. *Pontella valida* Dana occurred at only two stations, both located in high salinity ($>35.0^{0}/_{00}$) and relatively cool ($<27.2°$ C) surface waters, indicating that this species may be associated with the copepod fauna of West Central South Pacific surface waters (Sherman, 1964). The five "Albatross" locations at which *P. valida* occurred in the eastern Pacific, between 18° S to 25° S and 89° W to 124° W, were also characterized by high ($>35.0^{0}/_{00}$) surface salinities (Defant, 1961, pl. 5) and relatively cool waters, ranging from 27.2° C to 21.1° C (table II).

TABLE II

Station data and occurrence of *Pontella valida* Dana, "Albatross" Eastern Pacific cruise 1904-05

Station	Location		Date	Temperature ° C	Number of *Pontella valida*
4700	20° 29′ S	130° 26′ W	Dec. 25, 1904	23.3	9, females 9, males
4696	24° 40′ S	107° 05′ W	Dec. 23	23.3	2, females 3, males
4685	21° 36′ S	94° 56′ W	Dec. 10	21.6	1, female
4683	20° 02′ S	91° 52′ 30″ W	Dec. 9	21.1	1, male 1, female
4735	18° 16′ S	123° 34′ W	Jan. 22, 1905	27.2	1, female

ACKNOWLEDGEMENTS

I am grateful to Dr. Thomas E. Bowman, U. S. National Museum, Dr. George Grice, Woods Hole Oceanographic Institution, and Dr. Abraham Fleminger, Scripps Institution of Oceanography, for their reviews of the manuscript and helpful suggestions.

ZUSAMMENFASSUNG

Pontella valida Dana wird wiederbeschrieben. Es werden ferner Angaben über das Vorkommen dieser Art im zentralen Südpazifik und die dort herrschenden hydrographischen Bedingungen gemacht.

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SEASONAL OCCURRENCE OF LARVAL LOBSTERS IN COASTAL WATERS OF CENTRAL MAINE

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ABSTRACT

Seasonal occurrence of larval lobsters in coastal waters of central Maine was investigated in 4 years (1963-66). Larvae were most numerous in July and August.

The published record of larval lobsters, *Homarus americanus* Milne-Edwards, in coastal waters of Maine is limited to the report by Mendall (1934) of commercially important fish and shellfish in the stomachs of sea birds. The Bureau of Commercial Fisheries, in 1965, began a study of lobster populations in coastal and shelf waters off the northeastern United States. Our observations on occurrence of larvae were made as part of this investigation. Some information was available for earlier years from plankton collections made as part of other research.

Taylor (1950), using 10 years of hatchery records (1939-48), assigned June 1 to August 1 as the hatching period of lobsters held in tanks at Boothbay Harbor, Maine. Hatching in holding tanks begins earlier in southern New England and extends from late April to July (Herrick, 1911; Hughes and Matthiessen, 1962). These observations suggested that larvae could be present in coastal waters of Maine from spring through fall.

We examined zooplankton collected on bi-weekly cruises in the Boothbay Harbor area from May through October 1963, 1964, and 1965, for the presence of larval lobsters. The samples were originally designed to obtain larval herring; larval lobsters were captured incidentally. Samples were collected with a 1-meter net (0.36 mm apertures) towed just beneath the surface for 10 minutes at 2 knots. Of the 409 samples examined, 20 contained larval lobsters, but accounted for only 31 specimens. Although few larvae were collected, the occurrence within the season was similar in each of the three years. Larvae were taken most frequently during summer in July and August. No larvae were present in the May or October collections (Table 1).

The catch of larvae was increased in 1965 and 1966 by experimental towing at high speeds (4 to 6 knots). Three nets were used: a conical meter net and 2 rectangular trawls, one measuring 2 m x 1 m, and the other 1.5 m x 0.5 m at the mouth. Each was fitted with relatively wide-mesh netting (1-mm aperture). Surface tows were made with nets breaking the surface film. The rectangular trawls were towed with the widest mouth dimension in a horizontal plane. Duration of the tows varied from 10 to 30 minutes. A total of 257 surface tows were made at approximately bi-weekly intervals; 245 were from Casco Bay and the Boothbay area (Fig. 1), and 12 along the coast from Cape Ann, Massachusetts, to Machias Bay, Maine.

From June to September, 368 larvae were collected. Catches were highest in July and August (Table 1). This timing agrees with our findings from bi-weekly meter-net sampling. Evidence to show larval lobsters more abundant at the surface than a few feet below the surface has been presented by Templeman (1937), and Templeman and Tibbo (1945). Comparisons were made between catches with trawls at high speed (4 to 6 knots) at the surface and on oblique hauls through the water column (0-20 m) at 53 stations in 1966. Catches of larvae in the oblique tows were approximately 2.4 times less (17 larvae) than companion catches at the surface (40 larvae). It is likely that our increase in catch at high towing speeds in 1965 and 1966 was in part the result of towing at the air-sea interface.

The combined 1963-66 data agree with the July-August maximum of occurrence of larval lobsters in the Gulf of St. Lawrence (Wilder, 1953;

TABLE 1 . *Catches of lobster larvae from surface tows in central Maine waters, 1963-66.*

Year	Type of tow and number of larvae	Months May	June	July	August	September	October	Total
1963	Meter net[1]	12	35	24	14	26	8	—
	Number of larvae	0	1	3	5	0	0	—
1964	Meter net	20	18	20	20	24	37	—
	Number of larvae	0	2	4	4	3	0	—
1965	Meter net	43	14	27	33	10	24	—
	Number of larvae	0	0	5	4	0	0	—
1963-65	Number of tows	75	67	71	67	60	69	409
	Number of larvae	0	3	12	13	3	0	31
	Catch-per-tow	0	0.04	0.17	0.19	0.05	0	—
1965	High-speed[2]		10	97	24*	13	—	—
	Number of larvae		0	235	64	12	—	—
1966	High-speed	5	24	58	20	6	—	—
	Number of larvae	0	0	45	12	0	—	—
1965 66	Number of tows	5	34	155	44	19	—	257
	Number of larvae	0	0	280	76	12	—	368
	Catch-per-tow	0	0	1.81	1.73	0.63	—	—
1963-66	Total tows	80	101	226	111	79	69	666
	Total larvae	0	3	292	89	15	0	399

*12 of these samples were collected along the coast from Cape Ann, Massachusetts, to Machias Bay, Maine.

[1] Meter net tows were made with the nets just below the surface film.

[2] High speed tows were made with the nets breaking the surface film.

Corrivault and Tremblay, 1948), and with the finding of concentrations of larvae in coastal waters of Newfoundland in these same months (Templeman and Tibbo, 1945). Larvae also occur in offshore Gulf of Maine and continental shelf waters off New England in July and August. On a summer offshore cruise of the Bureau's research vessel *Albatross IV* (July 27 to August 4, 1966), 142 larvae were collected.

The number of days for the development of larvae from hatching to the end of the planktonic period at stage 4 varies with the temperature (Templeman, 1936; Hughes and Matthiesson, 1962). Average monthly surface temperatures in Boothbay Harbor ranged from 13.7°C to 15.0°C in July and August 1965 and 1966. At a temperature of 14.0°C the developmental period from hatching to stage 4 is 26 days; at 15.0°C, 22 days are required (Templeman, 1936). Larvae collected in the bi-weekly meter-net series from June through the first-half of August were all in developmental stage 1. Three stage 4 larvae were in later collections (August 26-September 2). The high-speed collections of 1965-66 contained stage 1 larvae most frequently in July, and stage 4 larvae in August and September (Table 2); apparently maximal hatching in coastal waters of central Maine was in July and early August.

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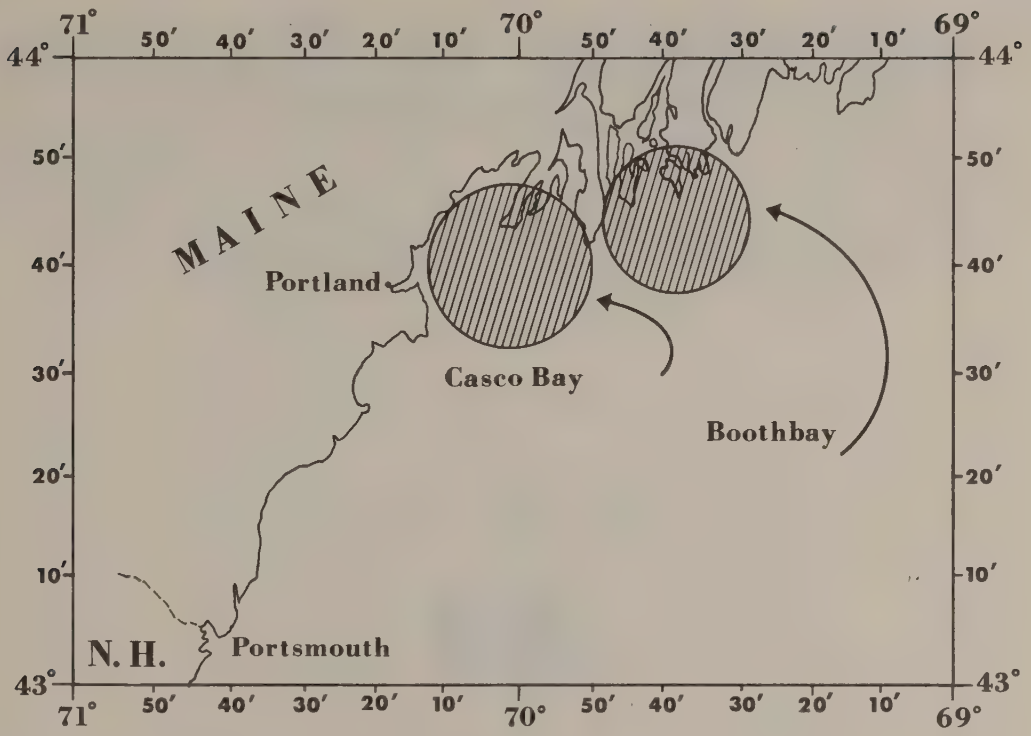
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20′
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43°
MAINE
Portland
Casco Bay
Boothbay
N. H.
Portsmouth

FIG. 1. *Coastal sampling areas for larval lobsters.*

TABLE 2. *Frequency of occurrence of developmental stages of larvae collected in high-speed tows, 1965 and 1966.*

Dates 1965-1966	Number of tows	Developmental stages* 1	 2	 3	 4
July 1-14	73				
Number of larvae		77			
Catch-per-tow		1.05			
July 15-29	82				
Number of larvae		198	2		3
Catch-per-tow		2.41	0.02		0.04
August 2-16	32				
Number of larvae		15	5	1	7
Catch-per-tow		0.46	0.16	0.03	0.22
August 14-20	12				
Number of larvae		6			42
Catch-per-tow		0.50			3.50
September 1-3	19				
Number of larvae					12
Catch-per-tow					0.63

*As described by Herrick, 1911.

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32

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Seasonal occurrence, distribution, and breeding of the chaetognath *Sagitta elegans* in coastal waters of Maine.

The chaetognath *Sagitta elegans* Verrill in the coastal waters of Maine undergoes seasonal fluctuations in abundance, progressing from a spring low to a summer high and declining in fall and winter. These fluctuations are related to the breeding cycle. One generation of *S. elegans* is produced annually. Breeding extends from spring through fall; the peak is in late spring. Maturing specimens dominate in winter (>80% of the population), and immature specimens in summer (75% of the population). Death of mature individuals after breeding appears to cause the spring population decline. Areal differences in abundance are influenced by the dominant non-tidal drift moving southwesterly along the Maine coast. In winter, when the drift is poorly developed, *S. elegans* is evenly distributed along the coast. Numbers increase progressively westward in summer and fall with the development of non-tidal drift; they reach an annual peak in the western area (Cape Elizabeth, Maine, to Cape Ann, Massachusetts) during fall. Concentrations of *S. elegans* along the coast are the result of local breeding. There is no evidence of large-scale transport of *S. elegans* to local areas from other breeding centers in the Gulf of Maine.

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PREDATION UPON PACIFIC HAKE, *MERLUCCIUS PRODUCTUS,* BY PACIFIC DOGFISH, *SQUALUS ACANTHIAS*

A mixed catch of Pacific hake and dogfish taken at Port Susan, Washington (an arm of Puget Sound, 30 nautical miles north of Seattle), on May 18, 1966, contained 20% by weight dogfish. The fish were schooled at 48 fathoms over a 65-fathom bottom, and were caught in a large midwater trawl by the U. S. Fish and Wildlife Service vessel *John N. Cobb* during an investigation of the hake resources in Puget Sound. A new commercial hake fishery was started in this area in the winter of 1965–66.

The hake in the catch ranged from 12 to 25 inches, with a mode of 14 inches, FL. In a random sample of 207 hake, 192 were males, a phenomenon that seems peculiar to the spawning period; usually the sexes are more evenly mixed. Most of the male hake were ripe, and milt flowed freely when the fish were lightly squeezed.

The dogfish were mostly large females, 2½ to 3 feet long, carrying young with attached yolk sacs. Of 52 dogfish stomachs examined, 25 contained hake. Most of the hake had been bitten neatly in two, and either the anterior, posterior, or both halves swallowed. Other species in the dogfish stomachs included Dungeness crab (*Cancer magister*) and Pacific herring (*Clupea harengus pallasii*).

Clemens and Wilby (1961) reported that dogfish appear in large numbers where herring school and that they feed on a variety of the smaller fishes. The observed feeding of dogfish on schooling hake is consistent with this behavior.

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—*Herbert H. Shippen and Miles S. Alton, U. S. Bureau of Commercial Fisheries, 2725 Montlake Blvd. E., Seattle, Washington 98102, August 1966.*

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PELAGIC FISHES CAUGHT ON R/V ANTON BRUUN CRUISES 2 AND 5 (INTERNATIONAL INDIAN OCEAN EXPEDITION)

by

R.S. Shomura

PELAGIC FISHES CAUGHT ON R/V ANTON BRUUN CRUISES 2 AND 5 (INTERNATIONAL INDIAN OCEAN EXPEDITION)

by

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ABSTRACT

During cruises 2 and 5 of the National Science Foundation research ship Anton Bruun in the Indian Ocean, scientists from the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, conducted longline fishing as part of the fishery phase of the U.S. biological effort in the International Indian Ocean Expedition. The catch consisted of 431 tunas (yellowfin, bigeye, skipjack, and albacore), 124 sharks, and 259 other fish. Additional specimens were taken by trolling (14), by rod and reel (61), and by hand line (14). Physical, chemical, and biological data were collected.

INTRODUCTION

From February 1963 to December 1964, the National Science Foundation research ship Anton Bruun (Fig. 1), operated in the Indian Ocean as part of the U.S. effort in the biological phase of the International Indian Ocean Expedition. This expedition, sponsored by United Nations Educational, Scientific and Cultural Organization, attempted to apply to a single ocean basin the kind of complex international scientific cooperation that produced such fruitful results during the International Geophysical Year. The Indian Ocean was selected as the area of study because, of all oceans, its submarine geology, physical and chemical oceanography, meteorology, and marine biology were the least known. Field work began in 1959 with scientific cruises by Australia, Russia, and the United States (Humphrey, 1963). By the end of 1965, the formal completion date of field work for the International Indian Ocean Expedition, 25 countries and about 40 research ships had participated in the program.

The Bureau of Commercial Fisheries carried out several studies on the fisheries of the Indian Ocean as part of the U.S. biological program sponsored by the National Science Foundation. The results of surveys of the benthic fish and invertebrates of the Bay of Bengal and the Arabian Sea have been published by Pruter (1964) and Hida and Pereyra (in press). This report presents information on the fishes caught on the R/V Anton Bruun cruise 2 (May-July 1963)

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and cruise 5 (January-May 1964). Table I lists the commonly accepted names of the pelagic fishes caught in the Indian Ocean.

PLAN OF WORK

Unlike some of the other scientific studies for which basic information was generally lacking, e.g., meteorology in the central Indian Ocean, the pelagic fishery program was developed with the knowledge that a high-seas fishery was already in operation there. The Japanese have had a commercial longline fishery since 1952. Initially, Japanese effort was concentrated in the eastern sector, where new fishing grounds for bluefin tuna were discovered (Mimura, 1958a). Since 1952 the Japanese longline fishery has expanded westward. It now extends from the coast of Australia to the coast of Africa and from about lat. 10°N to lat. 30°S. The tuna catch of the Japanese longline fishery in the Indian Ocean reached a high in 1956, when more than 100,000 metric tons of yellowfin, albacore, bigeye, and bluefin tuna were landed (Johnson, 1959). Since 1956 the landings have declined, owing in part to a decline in catch rates and in part to a shift of fishing effort into new tuna grounds discovered in the Atlantic. The decline in catch rates has been especially noticeable for the larger yellowfin tuna (Mimura, 1958b).

In view of the presence of an existing fishery, the research was directed towards collecting physical, chemical and biological data for a study of the distribution of commercially important pelagic fishes in relation to the environment. Tables II and III list the complete series of observations carried out on Anton Bruun cruise 2 and 5. On cruise 2 longline fishing was carried out at intervals from lat. 17°N to 37°S along long. 70°E and from lat. 30°S northward to Ceylon along long. 80°E (Fig. 2). On cruise 5 fishing extended from lat. 10°N to 36°S along long. 55°E and along long. 75°E from lat. 43°S to 4°N (Fig. 2); in addition, five fishing stations were occupied in the central Arabian Sea.

TABLE I

COMMONLY ACCEPTED NAMES OF FISHES TAKEN ON INDIAN OCEAN EXPEDITION OF THE ANTON BRUUN

Albacore - *Thunnus alalunga*
Barracuda - *Sphyraena sp.*
Bigeye tuna - *Thunnus obesus*
Black marlin - *Makaira indica*
Black skipjack tuna - *Euthynnus affinis*
Bluefin tuna - *Thunnus thynnus*
Blue marlin - *Makaira nigricans*
Bonito shark - *Isurus oxyrinchus*
Broadbill swordfish - *Xiphias gladius*
Dolphin - *Coryphaena hippurus*
Great blue shark - *Prionace glauca*
Lancetfish - *Alepisaurus brevirostris*
Lancetfish - *Alepisaurus ferox*
Little dolphin - *Coryphaena equiselis*
Opah - *Lampris regius*
Pelagic stingray - *Dasyatis violacea*
Sailfish - *Istiophorus gladius*
Salmon shark - *Lamna ditropis*
Sevengill shark - *Heptrachias sp.*
Shortbill spearfish - *Tetrapturus angustirostris*
Silky shark - *Carcharhinus falciformis*
Skipjack tuna - *Katsuwonus pelamis*
Snake mackerel - *Gempylus serpens*
Striped marlin - *Tetrapturus audax*
Thresher shark - *Alopias spp.*
Wahoo - *Acanthocybium solandri*
Whitetip shark - *Carcharhinus longimanus*
Yellowfin tuna - *Thunnus albacares*

TABLE II

SUMMARY OF SCIENTIFIC ACTIVITIES UNDERTAKEN ON ANTON BRUUN CRUISE 2

Station	Date 1963	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton new tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
106	5/23	17°39' N	70°25' E	x	x	x		x	x	x		
106A	5/23	17°04' N	70°23' E								x	x
107	5/24	15°41' N	70°07" E	x	x	x		x	x	x		
107A	5/24	15°01' N	70°09' E								x	x
108	5/25	13°50' N	70°07' E	x	x	x		x	x	x		
108A	5/25	13°15' N	70°03' E								x	x
109	5/26	11°59' N	69°55' E	x	x	x		x	x	x		
109A	5/26	11°28' N	69°56' E								x	x
110	5/27	09°47' N	70°04' E	x	x	x		x	x	x		
110A	5/27	09°26' N	69°59' E								x	x
111	5/28	08°09' N	70°02' E	x	x	x		x	x	x		
111A	5/28	07°08' N	69°57' E								x	x
112	5/29	05°48' N	70°02' E	x	x	x		x	x	x		
112A	5/29	04°58' N	70°01' E								x	x
113	5/30	03°32' N	69°54' E	x	x	x		x	x	x		
113A	5/30	02°46' N	69°54' E								x	x
114	5/31	01°30' N	69°59' E	x	x	x		x	x	x		
114A	5/31	01°16' N	70°20' E								x	x
115	6/1	01°07' S	70°55' E	x	x	x		x	x	x		
115A	6/1	01°10' S	71°08' E								x	x
116	6/2	02°24' S	70°24' E	x	x	x		x	x	x		
116A	6/2	02°57' S	70°00' E								x	x
117	6/3	04°22' S	69°26' E		x	x		x	x	x		
117A	6/3	05°54' S	69°47' E								x	x
118	6/4	06°47' S	70°17' E		x			x	x	x		
118A	6/4	06°37' S	70°09' E								x	x
118B	6/5	06°45' S	69°41' E	x		x						
119	6/6	08°35' S	69°55' E	x	x					x		
119A	6/6	09°26' S	70°03' E								x	

TABLE II (con.)

Station	Date 1963	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Be net)	Oblique plankton new tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
120	6/7	11°10' S	70°02' E		x	x		x		x		
120A	6/7	12°04' S	70°02' E								x	x
121	6/8	13°15' S	69°51' E	x	x		x	x	x	x		
121A	6/8	14°14' S	70°02' E								x	x
122	6/9	15°25' S	69°58' E	x	x	x		x	x	x		
122A	6/9	16°08' S	70°02' E								x	x
123	6/10	17°18' S	70°05' E	x	x	x		x	x	x		
123A	6/10	18°12' S	70°04' E								x	x
124	6/11	19°30' S	69°51' E	x	x	x		x	x	x		
124A	6/11	19°32' S	68°46' E								x	x
124B1/	6/12	19°30' S	63°50' E								x	x
124C	6/13	19°27' S	58°51' E								x	x
124D1/	6/14	19°47' S	57°28' E									
124E1/	6/14	19°54' S	57°36' E									
124F	6/24	21°21' S	65°52' E								x	x
125	6/25	21°41' S	67°08' E	x	x		x	x	x	x		
125A	6/25	22°37' S	68°04' E								x	x
126	6/26	23°47' S	69°05' E	x	x	x		x	x	x		
126A	6/26	25°01' S	69°30' E								x	x
127	6/27	26°34' S	70°12' E	x	x	x		x	x	x		
127A	6/27	27°23' S	70°04' E								x	x
128	6/28	28°30' S	69°52' E	x	x		x	x		x		
128A	6/28	29°11' S	69°57' E								x	x
129	6/29	30°34' S	69°55' E	x	x	x		x	x	x		
129A	6/29	31°28' S	69°52' E								x	x
130	6/30	32°53' S	69°52' E	x	x	x		x	x	x		
130A	6/30	33°42' S	69°56' E								x	x
131	7/1	35°09' S	69°59' E	x	x	x		x	x	x		
131A	7/1	35°57' S	70°04' E								x	x
132	7/2	37°12' S	70°11' E	x	x	x		x	x	x		

Explanation of footnote at end of table.

TABLE 11 (con.)

Station	Date 1963	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton new tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
132A	7/2	36°52' S	70°39' E								x	x
132B	7/3	35°17' S	72°55' E			x						
132C	7/3	34°06' S	74°26' E								x	x
132D	7/4	31°08' S	78°28' E								x	x
133	7/5	30°11' S	79°43' E	x	x	x		x	x	x		
133A	7/5	29°24' S	79°48' E								x	x
134	7/6	27°31' S	80°07' E		x	x		x	x	x		
134A	7/6	26°17' S	80°10' E								x	x
134B	7/7	21°37' S	79°55' E								x	x
135	7/8	20°04' S	79°49' E	x	x	x		x	x	x		
135A	7/8	18°59' S	79°53' E								x	x
136	7/9	17°15' S	79°53' E		x	x		x				
137	7/10	14°36' S	79°49' E	x	x		x	x		x		
137A	7/10	13°40' S	79°48' E								x	x
138	7/11	11°29' S	79°55' E		x		x	x		x		
138A	7/11	10°08' S	79°48' E								x	x
139	7/12	08°35' S	79°32' E	x	x		x	x		x		
139A	7/12	07°24' S	79°42' E								x	x
140	7/13	05°53' S	79°57' E		x	x		x	x	x		
140A	7/13	04°41' S	80°01' E								x	x
141	7/14	03°19' S	80°04' E	x	x		x	x	x	x		
141A	7/14	02°03' S	80°08' E								x	x
142	7/15	00°34' S	80°05' E	x	x		x	x	x	x		
142A	7/15	00°23' N	79°58' E								x	x
143	7/16	01°53' N	79°52' E	x	x	x		x	x	x		
143A	7/16	02°51' N	79°53' E								x	x
144	7/17	04°19' N	80°05' E	x	x	x		x	x	x		
144A	7/17	05°01' N	80°05' E								x	x
144B	7/19										x	
144C	7/20										x	
144D	7/21										x	

1/ Unlisted activities were: a midwater trawl haul at station 124B, night-light fishing at 124D, and two dredge hauls at 124E.

TABLE III

SUMMARY OF SCIENTIFIC ACTIVITIES UNDERTAKEN ON ANTON BRUUN CRUISE 5

Station	Date 1964	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton net tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night) Surface	1-m plankton net tow (night) Oblique
281X	1/27	17°44' N	69°11' E								x	x
281Y	1/28	16°44' N	65°08' E								x	x
282	1/29	16°13' N	63°29' E	x	x	x		x	x	x		
282A	1/29	16°03' N	62°16' E								x	x
283	1/30	15°42' N	60°52' E	x	x	x		x	x	x		
283A	1/30	15°35' N	60°04' E								x	x
284	1/31	15°22' N	58°12' E		x	x		x	x	x		
284A	1/31	15°04' N	56°51' E								x	
285	2/1	14°22' N	54°18' E	x	x	x		x	x	x		
285A	2/1	14°02' N	54°08' E								x	x
286	2/2	13°50' N	52°59' E	x	x	x		x	x	x		
286A	2/2	13°40' N	51°54' E								x	x
287	2/3	13°11' N	50°22' E	x	x	x		x	x	x		
287A	2/3	12°40' N	51°13' E								x	x
287B1/	2/4	10°21' N	54°17' E								x	x
288	2/5	09°28' N	54°52' E	x	x	x		x	x	x		
288A	2/5	08°29' N	54°56' E								x	x
289	2/6	07°10' N	55°05' E	x	x	x		x	x	x		
289A	2/6	06°28' N	55°04' E								x	x
290	2/7	05°02' N	55°01' E		x		x	x	x	x		
290A	2/7	03°54' N	55°01' E								x	x
291	2/8	02°31' N	55°04' E		x	x		x	x	x		
291A	2/8	01°58' N	54°57' E								x	x
292	2/9	01°03' N	54°46' E	x	x	x		x		x		
292A	2/9	00°37' N	54°54' E								x	x
293	2/10	00°31' S	54°56' E	x	x		x	x	x	x		
293A	2/10	01°15' S	54°52' E								x	x
294	2/11	02°51' S	54°58' E	x	x	x		x	x	x		

Explanation of footnote at end of table.

TABLE III (Con.)

Station	Date 1964	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton net tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
294A1/	2/11	03°37' S	55°22' E								x	
294B	2/15	05°09' S	55°26' E								x	
295	2/16	06°28' S	55°12' E	x	x	x		x	x	x		
295A	2/16	07°34' S	55°10' E								x	x
296	2/17	08°42' S	55°07' E	x	x	x		x	x	x		
296A	2/17	09°32' S	55°12' E								x	x
297	2/18	10°47' S	55°15' E	x	x	x		x	x	x		
297A	2/18	11°18' S	54°59' E								x	x
298	2/19	12°33' S	54°33' E	x	x	x		x	x	x		
298A	2/19	13°37' S	54°43' E								x	x
299	2/20	14°57' S	54°43' E	x	x		x	x	x	x		
299A	2/20	16°04' S	54°50' E								x	x
300	2/21	17°14' S	54°38' E	x	x	x		x	x	x		
300A	3/2	20°02' S	56°13' E								x	x
301	3/3	19°57' S	54°58' E	x	x	x		x	x	x		
301A	3/3	21°08' S	54°55' E								x	x
302	3/4	23°07' S	54°50' E		x	x		x	x	x		
302A	3/4	24°39' S	54°57' E								x	x
303	3/5	26°00' S	54°52' E	x	x	x		x		x		
303A	3/5	26°56' S	55°01' E									x
304	3/6	28°22' S	55°02' E	x	x	x		x	x	x		
304A	3/6	29°31' S	55°09' E								x	x
305	3/7	30°50' S	55°02' E	x	x	x		x	x	x		
305A	3/7	31°56' S	54°59' E								x	x
306	3/8	33°13' S	55°10' E	x	x	x		x	x	x		
306A	3/8	34°25' S	55°06' E								x	x
307	3/9	35°42' S	55°15' E	x	x	x		x	x	x		
307A	3/29	23°21' S	58°52' E								x	x
307B	3/30	26°34' S	61°31' E								x	x
307C	3/31	29°46' S	64°-2' E								x	x

Explanation of footnote at end of table.

TABLE III (Con.)

Station	Date 1964	Latitute	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton net tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
307D	4/1	32°56' S	67°23' E								x	x
307E	4/2	35°45' S	70°36' E								x	x
307F	4/3	38°51' S	74°02' E								x	x
308	4/4	40°04' S	75°00' E	x	x	x		x	x	x		
308A	4/4	41°01' S	75°00' E								x	x
309	4/5	42°23' S	74°54' E	x	x	x		x		x		
309A	4/5	43°01' S	75°03' E								x	x
309B	4/6	41°42' S	76°34' E								x	x
309C1/	4/7	St. Paul Island										
309D	4/7	38°18' S	77°38' E								x	x
309E1/	4/8	Amsterdam Island										
310	4/9	37°01' S	75°19' E	x	x	x		x	x	x		
310A	4/9	35°50' S	75°07' E								x	x
311	4/10	34°31' S	74°47' E	x	x	x		x	x	x		
311A	4/10	33°22' S	74°56' E								x	x
312	4/11	31°26' S	74°57' E		x	x		x	x	x		
312A	4/11	30°09' S	74°58' E								x	x
313	4/12	29°00' S	74°51' E	x	x	x			x	x		
313A	4/12	27°50' S	75°03' E								x	x
314	4/13	26°27' S	75°02' E	x	x	x		x	x	x		
314A	4/13	25°37' S	75°02' E								x	x
315	4/14	24°20' S	74°52' E	x	x	x		x		x		
315A	4/14	23°26' S	75°01' E								x	x
316	4/15	21°58' S	74°55' E	x	x	x		x		x		
316A	4/15	21°13' S	75°17' E								x	x
317	4/16	19°44' S	75°20' E	x	x	x		x	x	x		
317A	4/16	18°46' S	75°13' E								x	x
318	4/17	16°43' S	74°53' E		x	x		x	x	x		
318A	4/17	15°39' S	74°52' E								x	x

Explanation of footnote at end of table.

TABLE III (con.)

Station	Date 1964	Latitude	Longitude	Longline fishing	Hydrocast	Multiple plankton net tow (Bé net)	Oblique plankton net tow	Indian Ocean standard net (vertical tow)	Micronet (vertical tow)	Primary productivity	1-m plankton net tow (night)	
											Surface	Oblique
319	4/18	14°10' S	74°55' E	x	x	x		x	x	x		
319A	4/18	13°14' S	74°57' E								x	x
320	4/19	11°47' S	74°42' E	x	x	x		x	x	x		
320A	4/19	10°44' S	74°56' E								x	x
321	4/20	09°21' S	75°08' E	x	x	x		x	x	x		
321A	4/20	08°19' S	75°09' E								x	x
322	4/21	06°50' S	75°02' E	x	x	x		x	x	x		
322A	4/21	05°43' S	74°59' E								x	x
323	4/22	04°11' S	75°00' E	x	x	x		x	x	x		
323A	4/22	03°40' S	75°05' E								x	x
324	4/23	02°14' S	75°14' E	x	x	x		x	x	x		
324A	4/23	01°35' S	74°41' E								x	x
325	4/28	01°04' S	75°07' E		x		x	x	x	x		
325A	4/28	02°28' S	75°10' E								x	x
326	4/29	03°52' S	74°57' E	x	x	x		x	x	x		
326A	4/29	04°49' S	74°55' E								x	x
327	4/30	06°51' S	75°02' E		x	x		x	x	x		
327A	4/30	08°21' S	75°34' E								x	x
327B	5/2										x	
327C	5/										x	
327D	5/4										x	

1/ Unlisted activities were: midwater trawl hauls at stations 287B and 294A, sea bird and fish collection at station 309C, and fish collection at station 309E.

GEAR AND PROCEDURES

The principal fishing gear was the Japanese-type longline. Shapiro (1950) gave an excellent description of the development of the longline gear in Japan, and Niska (1953) provided details on the construction of the longline gear used at the Biological Laboratory in Honolulu. Basically, longline gear consists of a series of mainline sections suspended in the water at intervals by floats. Spearate hook lines are attached at intervals on the mainline. Figure 3 shows a schematic diagram of a unit of longline gear (commonly referred to as a basket of gear) used on the Anton Bruun.

From 40 to 50 baskets of longline gear were set at dawn (Tables IV and V), baited with frozen saury (*Cololabis saira*) 15 to 20 cm long. The operation was carried out from the stern of the ship, and took about 1 hour.

Upon completion of setting, the gear was allowed to fish for about 5 hours before hauling began. During this period other scientific activities were carried out on board the ship. Collections and observations routinely made at each station consisted of: (1) a hydrographic cast down to 2,000 m, (2) a multi-depth zooplankton net tow, (3) a vertical microplankton net tow from 200 m to the surface, (4) a vertical zooplankton net tow from 200 m to the surface, and (5) primary productivity studies (Carbon 14 and pigment analyses). The results of these studies will be published elsewhere.

Hauling of the longline gear usually started at noon and required about 2-1/2 hours for 50 baskets of gear. Hauling was carried out on the main deck along the starboard passageway, about one-third aft of the bow. Because the passageway was extremely narrow, a section of the bulwark was hinged, so that it could be lowered to deck level and thus increase the work area. When fishing, a removable safety rail of steel pipe was placed along the outer edge of the lowered platform. The rail served as an attachment for the longline roller, which permitted free movement of the mainline over the rail when hauling.

Two methods were used in hauling the longline catch. Fish up to about 60 kg were hauled from a platform aft of the longline hauler and about 1 m above the waterline (Figs. 4 and 5). Heavier fish were guided to the stern of the ship. On cruise 2 various methods, e.g., harpoon, rope noose, long gaff, and flying gaff, were employed in landing the fish from the stern. None worked satisfactorily and many fish were lost. The problem of handling large fish was solved on cruise 5 by using a large (1.2 m by 2.4 m) rectangular net (Fig 6). The rig was lowered and raised by a hydraulic crane on the starboard side of the ship, in an open afterdeck area. The largest fish landed by this method was a 229-kg black marlin (Fig. 7).

Detailed records were kept on the longline operation and the catch. Operational aspects of the longline fishing are summarized in Table IV and V. During hauling an observer close to the longline hauler recorded information on the catch, or the presence or absence of bait, for each hook as it was retrieved. If a fish was hooked, the data collected included the hook number and basket number, the species and the general condition of the fish (alive, dead or damaged by sharks).

TABLE IV

SCHEDULE OF LONGLINE FISHING, R/V ANTON BRUUN CRUISE 2

Sta. no.	Date (1963)	Noon position		Gear		Setting time[1]		Hauling time	
		Latitude	Longitude	No. of baskets	No. of hooks	Start	End	Start	End
106	5/23	17°39' N	70°25' E	20	112	0748	0845	1526	1731
107	5/24	15°41' N	70°07' E	40	242	0526	0705	1421[2]	1712
108	5/25	13°50' N	70°07' E	40	242	0515	0628	1455	1715
109	5/26	11°59' N	69°55' E	40	242	0517	0629	1459	1740
110	5/27	09°47' N	70°04' E	40	242	0515	0614	1506	1810
111	5/28	08°09' N	70°02' E	40	242	0440	0535	1250	1540
112	5/29	05°48' N	70°02' E	41	248	0430	0528	1320	1552
113	5/30	03°32' N	69°54' E	40	242	0430	0528	1407	1629
114	5/31	01°30' N	69°59' E	40	242	0429	0528	1246	1511
115	6/1	01°07' S	70°55' E	40	242	0427	0525	1729	1950
116	6/2	02°24' S	70°24' E	40	242	0635	0733	1514	1730
118B	6/5	06°45' S	69°41' E	40	191[3]	0447	0547	1104	1315
119	6/6	08°35' S	69°55' E	40	242	0515	0615	1240	1519
121	6/8	13°15' S	69°51' E	40	242	0515	0610	1212	1420
122	6/9	15°25' S	69°58' E	40	242	0500	0555	1408	1607
123	6/10	17°18' S	70°05' E	40	242	0504	0550	1306	1531
124	6/11	19°30' S	69°51' E	40	242	0505	0555	1330	1545
125	6/25	21°41' S	67°08' E	40	242	0534	0630	1239	1436
126	6/26	23°47' S	69°05' E	40	242	0532	0627	1218	1415
127	6/27	26°34' S	70°12' E	40	242	0532	0640	1404	1615
128	6/28	28°30' S	69°52' E	40	242	0700	0750	1231	1445
129	6/29	30°34' S	69°55' E	40	242	0532	0630	1356	1558
130	6/30	32°53' S	69°52' E	40	242	0537	0630	1431	1630
131	7/1	35°09' S	69°59' E	40	242	0623	0720	1444	1637
132	7/2	37°12' S	70°11' E	40	242	0534	0628	1334	1545
133	7/5	30°11' S	79°43' E	40	242	0540	0635	1405	1606
135	7/8	20°04' S	79°49' E	40	242	0532	0627	1236	1439
137	7/10	14°36' S	79°49' E	40	242	0540	0635	1209	1440
139	7/12	08°35' S	79°32' E	40	242	0534	0628	1132	1355
141	7/14	03°19' S	80°04' E	40	242	0532	0626	1129	1325
142	7/15	00°34' S	80°05' E	40	242	0531	0628	1246	1446
143	7/16	01°53' N	79°52' E	40	242	0530	0630	1229	1424
144	7/17	04°19' N	80°05' E	40	242	0531	0626	1429	1629

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[1] Local time.

[2] Hauling procedure reversed; first basket hauled was the first basket set in the morning.

[3] Eight baskets of gear with an additional 51 hooks were lost as result of a break in the mainline.

TABLE V

SCHEDULE OF LONGLINE FISHING, R/V *ANTON BRUUN* CRUISE 5

Sta. no.	Date (1964)	Noon position		Gear		Setting time		Hauling time	
		Latitude	Longitude	No. of baskets	No. of hooks	Start	End	Start	End
282	1/29	16°13' N	63°29' E	30	182	0501	0559	1240	1410
283	1/30	15°42' N	60°52' E	50	302	0500	0637	1315	1542
285	2/1	14°22' N	54°18' E	50	302	0515	0638	1204	1440
286	2/2	13°50' N	52°59' E	50	302	0500	0624	1213	1445
287	2/3	13°11' N	50°22' E	50	302	0528	0652	1300	1521
288	2/5	09°28' N	54°52' E	50	302	0500	0619	1300	1529
289	2/6	07°10' N	55°05' E	50	302	0500	0618	1309	1540
292	2/9	01°03' S	54°46' E	40	242	0530	0605	1515	1717
293	2/10	00°31' S	54°56' E	40	242	0511	0618	1130	1348
294	2/11	02°51' S	54°58' E	40	242	0505	0609	1224	1423
295	2/16	06°28' S	55°12' E	50	302	0500	0620	1343	1618
296	2/17	08°42' S	55°07' E	40	242	0502	0603	1322	1551
297	2/18	10°47' S	55°15' E	40	241	0459	0604	1338	1705
298	2/19	12°33' S	54°33' E	40	242	0507	0610	1237	1436
299	2/20	14°57' S	54°43' E	40	242	0501	0602	1205	1404
300	2/21	17°14' S	54°38' E	40	242	0504	0603	1248	1520
301	3/3	19°57' S	54°58' E	40	242	0503	0602	1245	1456
303	3/5	26°00' S	54°52' E	40	242	0500	0557	1320	1530
304	3/6	28°22' S	55°02' E	40	242	0513	0605	1235	1434
305	3/7	30°50' S	55°02' E	40	242	0505	0557	1227[1]	1421
306	3/8	33°13' S	55°10' E	40	242	0502	0548	1212	1410
307	3/9	35°42' S	55°15' E	39	236	0459	0550	1219	1408
308	4/4	40°04' S	75°00' E	50	302	0505	0608	1231	1515
309	4/5	42°23' S	74°54' E	50	300	0500	0600	1404	1659
310	4/9	37°01' S	75°19' E	40	242	0506	0548	1233	1444
311	4/10	34°31' S	74°47' E	50	302	0459	0557	1212	1444
313	4/12	29°00' S	74°51' E	50	302	0459	0554	1200	1426
314	4/13	26°27' S	75°02' E	50	302	0530	0635	1305	1538
315	4/14	24°20' S	74°52' E	50	302	0530	0643	1254	1519
316[2]	4/15	21°58' S	74°55' E	19	115	0555	0620	0905	1000
317	4/16	19°44' S	75°20' E	50	302	0527	0625	1244	1520
319	4/18	14°10' S	74°55' E	50	302	0529	0623	1256	1522
320	4/19	11°47' S	74°42' E	50	302	0527	0623	1233	1505
321	4/19	09°21' S	75°08' E	50	302	0528	0622	1227	1459
322	4/21	06°50' S	75°02' E	40	242	0528	0610	1212	1414
323	4/22	04°11' S	75°00' E	50	302	0528	0623	1258	1555
324	4/23	02°14' S	75°14' E	40	242	0539	0619	1245	1502
326	4/29	03°52' N	74°57' E	50	302	0527	0625	1204	1435

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[1] Hauling sequence reversed; first basket hauled first basket set.

[2] Mainline parted during setting operation; gear retrieved early because of rough weather.

As soon as a fish was landed an identifying number was tied to its tail, to simplify record keeping. Each fish was subjected to different type of examination and certain basic information (e.g., species, length, weight and sex) was needed for each examination. Some specimens were preserved whole for taxonomic studies, but after pertinent data and material were collected, most fish were discarded or frozen for later disposition (e.g., to charitable institutions). The biological material collected from each fish varied, and included blood samples from tunas for serological studies, parasitic copepods, parasitic trematodes (external and internal), ovaries, and stomach contents.

The longline catches by stations are summarized in Tables VI and VII.

OTHER METHODS OF FISHING

Other methods of fishing employed on both cruises, as circumstances permitted, were trolling and fishing with rod and reel and with hand lines. For trolling two lines were usually trailed from the stern of the Anton Bruun during daylight while the ship was under way between stations. A variety of feathered lures was employed. Table VIII presents data on fish caught with trolling gear. That small numbers of fish were caught by trolling may be primarily attributed to the speed of the vessel, which on runs between stations generally exceeded 11 knots.

A second incidental method, which proved to be more productive, was rod-and-reel fishing while the Anton Bruun drifted on station. In addition to providing the ship's complement with a recreational outlet, the fish specimens collected were extremely interesting and valuable (Table IX). The small tunas taken by rod and reel are not generally caught with the longline gear. Also, the little dolphin was taken only by rod and reel on both cruises.

Hand-line fishing was done sporadically and only for catching sharks while the ship drifted on station. Only whitetip sharks were caught by this method--10 on cruise 2 and 4 on cruise 5.

PRESENT AND FUTURE STUDIES

Detailed data on the fish catch of the two Anton Bruun cruises have been submitted to World Data Center A (Washington, D.C., U.S.A.) and the Fishery Data Center of the Food and Agricultural Organization of the United Nations.

The biological material collected on the cruise is currently being analyzed. Following is a brief summary of the status of these studies in July 1966.

A study of the gonad material has been completed. Since we do not expect to collect additional gonad material from the Indian Ocean, the data have been analyzed and a short technical paper has been prepared for submission at the 12th Session of the Indo-Pacific Fishery Council (Kikawa, S., and Ferraro, M.G. MS1/).

1/ Kikawa, S. and Ferraro, M.G. (MS). Notes on the Maturation of Tunas in the Indian Ocean. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

TABLE VI

SUMMARY OF LONGLINE CATCH, R/V *ANTON BRUUN* CRUISE 2

Station	Yellowfin tuna	Bigeye tuna	Albacore	Skipjack tuna	Blue marlin	Striped marlin	Sailfish	Whitetip shark	Silky shark	Thresher shark	Great blue shark	Bonito shark	Lancetfish	Others
106						3	1	1		1		1		
107						2			4			1		
108					2				2			1		
109					1	1	1	1	7	2		1	2	
110	1	4						6	14	1		4		
111		1		2			1	2	1	1			1	
112	2	1		1	1			1	1			1	1	
113	1						1	2						1 snake mackerel; 2 barracuda.
114	44											1	1	1 unidentified tuna (eaten by sharks); 1 pelagic stingray.
115	7				1					1				
116	6	1			3			1					1	
118B	2	2					1	2						
119		2			1			1		2			5	2 shortbill spearfish.
121	1	1		1									14	1 barracuda; 1 dolphin.
122			2										6	1 dolphin.
123		3	4									2	6	1 wahoo.
124	2	1	9								1		1	
125	2		5					1					1	
126			3											
127	1		9			1							3	1 shortbill spearfish.
128	2		3	1										
129	1		1										6	
130		5	3											1 opah.
131			3								2		2	
132			2								9	1		
133	1		2	1									1	
136	1		2	3									1	1 wahoo.
137	4		3										3	1 black marlin; 1 shortbill spearfish.
139	7	2			2			1		1		1	1	1 shortbill spearfish.
141	3	1											1	1 dolphin.
142	5					1							2	
143	6					1	1							
144	1			1	2	1		1	3				1	
	100	24	51	10	13	10	6	20	32	9	12	14	60	18

TABLE VII

SUMMARY OF LONGLINE CATCH, R/V ANTON BRUUN CRUISE 5

Station	Yellowfin tuna	Bigeye tuna	Albacore	Skipjack tuna	Blue marlin	Striped marlin	Sailfish	Whitetip shark	Silky shark	Thresher shark	Great blue shark	Bonito shark	Lancetfish	Others
282										1		1		
283														
285	1			1										
286														
287	2													1 sevengill shark.
288		5				1				1				
289		2					1		1	2		1		
292		1				1			1		1		16	2 barracuda.
293	9	1		1		2	1	1			1		4	
294	3												2	
295	18	2					2	2			1			1 wahoo.
296	7	2	1				2					1	5	1 barracuda.
297	3	2	2					2					5	1 black marlin; 1 barracuda.
298	4						1						6	1 wahoo.
299	2		1										5	1 shortbill spearfish; 1 barracuda; 1 dolphin.
300	4		2										11	1 broadbill swordfish.
301	2		1		1								2	1 broadbill swordfish; 1 wahoo; 1 barracuda.
303	6	1	1			1							2	1 shortbill spearfish.
304	3		1										3	
305			3										1	
306	1	1	1								1		1	
307	1												1	
308		3	18											
309		12	1								3			2 salmon shark.
310			3									1		
311			9								1			1 wahoo.
313	2		5										4	
314			9										4	1 shortbill spearfish.
315	1	1	4										4	
316[1/]													1	
317	1		5										2	1 black marlin.
319			4			1							3	1 unidentified shark (family Isuridae); 1 dolphin.
320	3	6	9								1		5	
321	3	3	3										7	1 broadbill swordfish.
322	1	5				1		1	1				4	1 opah.
323	12	3			1			3					4	1 dolphin.
324	14	1		1							1		1	
326	2	3			2		1	2	1				9	
	105	54	83	3	4	7	8	11	4	4	10	4	112	26

1/ Mainline parted during setting operations; gear retrieved early because of bad weather.

TABLE VIII

SUMMARY OF CATCH BY TROLLING, R/V *ANTON BRUUN* CRUISES 2 AND 5

Date	Species	Position		Fork length (cm)
		Lat.	Long.	
	Cruise 2			
12 June 1963	Dolphin	19°32' S	65°34' E	93.4
13 June 1963	Yellowfin tuna	19°24' S	62°02' E	96.9
13 June 1963	Yellowgin tuna	19°24' S	61°42' E	65.6
	Cruise 5			
28 Jan. 1964	Carangid (unidentified)	17°11' N	66°52' E	--
2 Feb. 1964	Skipjack tuna	13°46' N	52°24' E	50.4
7 Feb. 1964	Dolphin	04°13' N	55°01' E	67.3
10 Feb. 1964	Skipjack tuna	00°52' S	54°49' E	45.5
15 Feb. 1964	Black skipjack tuna	04°54' S	55°32' E	64.5
15 Feb. 1964	Black skipjack tuna	04°54' S	55°32' E	67.3
15 Feb. 1964	Dolphin	04°54' S	55°32' E	80.0
2 Mar. 1964	Yellowfin tuna	20°03' S	56°38' E	74.6
12 Mar. 1964	Dolphin	27°02' S	55°46' E	86.8
12 Mar. 1964	Dolphin	27°02' S	55°46' E	82.2
28 Apr. 1964	Yellowfin tuna	02°02' N	75°13' E	54.6

TABLE IX

SUMMARY OF CATCH WITH ROD AND REEL, R/V *ANTON BRUUN* CRUISES 2 AND 5

Date	Species	Position		Number caught	Range in fork length (cm)
		Lat.	Long.		
	Cruise 2				
25 May 1963	Little dolphin	13°50' N	70°07' E	6	23.3-28.7
27 May 1963	Little dolphin	09°47' N	70°04' E	1	24.8
27 May 1963	Yellowfin tuna	09°47' N	70°04' E	3	24.0-29.6
28 May 1963	Little dolphin	08°09' N	70°01' E	1	28.4
28 May 1963	Yellowfin tuna	08°09' N	70°01' E	4	30.6-34.1
28 May 1963	Skipjack tuna	08°09' N	70°01' E	1	28.2
4 June 1963	Carangid (unidentified)	06°47' S	70°18' E	1	66.0
14 June 1963	Dolphin	03°19' S	80°06' E	2	79.5-80.3
15 July 1963	Dolphin	00°34' S	80°05' E	3	85.6-95.6
	Cruise 5				
6 Feb. 1964	Little dolphin	07°10' N	55°05' E	2	32.1[1]
6 Feb. 1964	Dolphin	07°10' N	55°05' E	10	57.4-74.3
8 Feb. 1964	Dolphin	02°31' N	55°04' E	1	82.0
4 Mar. 1964	Dolphin	23°07' S	54°50' E	14	71.7-82.3
17 Apr. 1964	Barracuda	16°43' S	74°53' E	1	No length data
23 Apr. 1964	Dolphin	02°14' S	75°14' E	11	82.0-95.8

1/ One fish was not measured.

On both Anton Bruun cruises the stomach contents of most of the pelagic fishes caught by the different fishing methods were preserved for detailed studies. The identification and measurement of this material is nearly complete.

The major effort in the analysis of the Indian Ocean material will be centered on a comprehensive study on the distribution and abundance of pelagic fishes in relation to the environment. This cooperative study is being carried out by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, and the Nankai Regional Fisheries Research Laboratory in Japan. The materials to be examined will include fishing and environmental data collected on the two cruises of the Anton Bruun, data from the Japanese commercial fishery in the Indian Ocean, and oceanographic data from the U.S. National Oceanographic Data Center.

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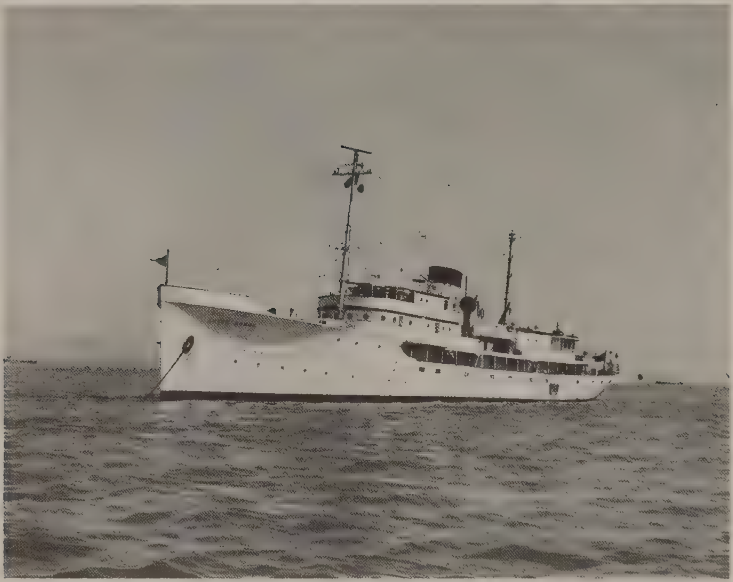
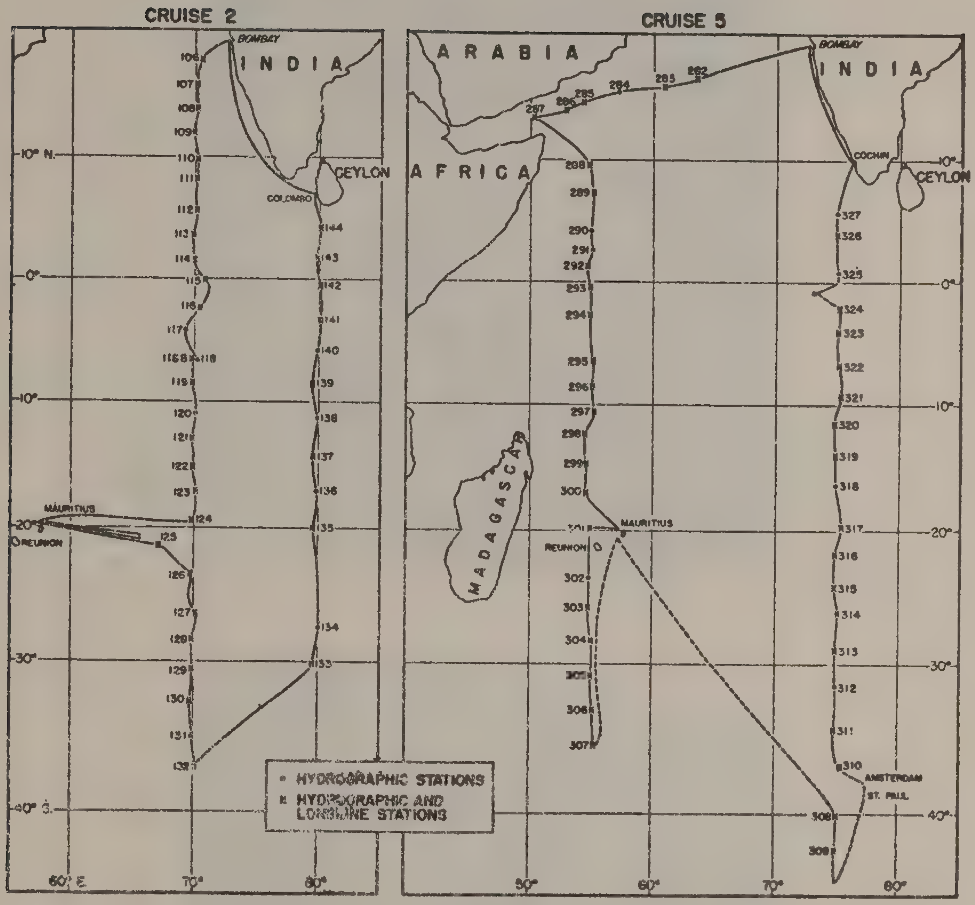


Fig. 1. U.S. National Science Foundation Research Ship
Anton Bruun at Anchor in Bombay (India) Harbor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CRUISE 5
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• HYDROGRAPHIC STATIONS
x HYDROGRAPHIC AND LONGLINE STATIONS

Fig. 2. Cruise Tracks of R/V Anton Bruun Cruise 2 (22 May-23 July 1963) and Cruise 5 (26 January-4 May 1964)

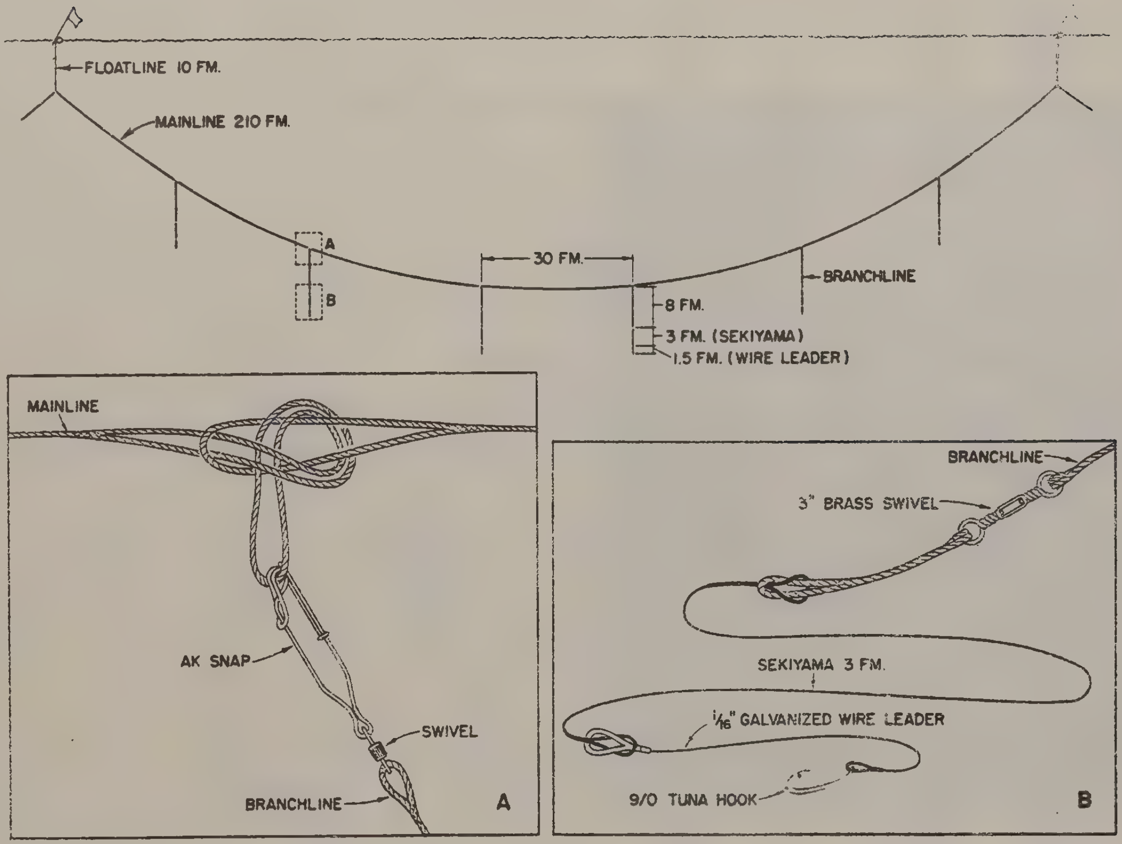
FLOATLINE 10 FM.
MAINLINE 210 FM.
A
B
30 FM.
BRANCHLINE
8 FM.
3 FM. (SEKIYAMA)
1.5 FM. (WIRE LEADER)
MAINLINE
AK SNAP
SWIVEL
BRANCHLINE
A
BRANCHLINE
3" BRASS SWIVEL
SEKIYAMA 3 FM.
1/16" GALVANIZED WIRE LEADER
9/0 TUNA HOOK
B

Fig. 3. Schematic Diagram of Longline Gear Used on R/V *Anton Bruun* Cruises 2 and 5

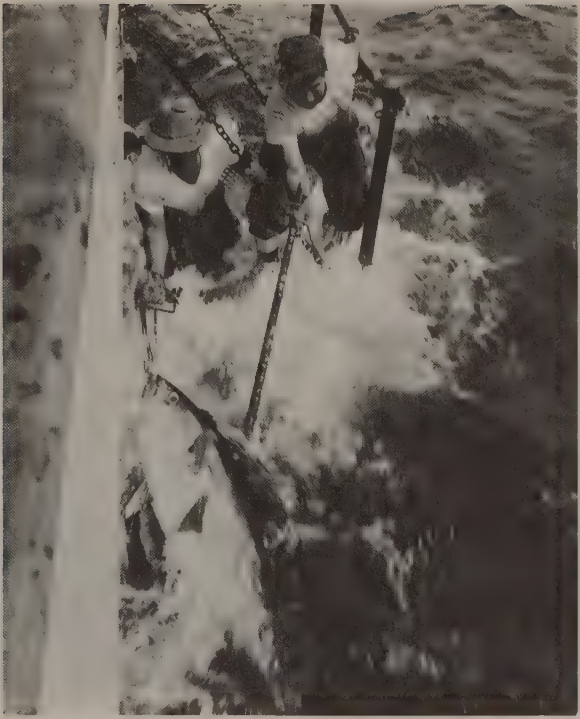

Fig. 4. Gaffing Tuna Caught on a Longline from the Lowered Platform on R/V Anton Bruun

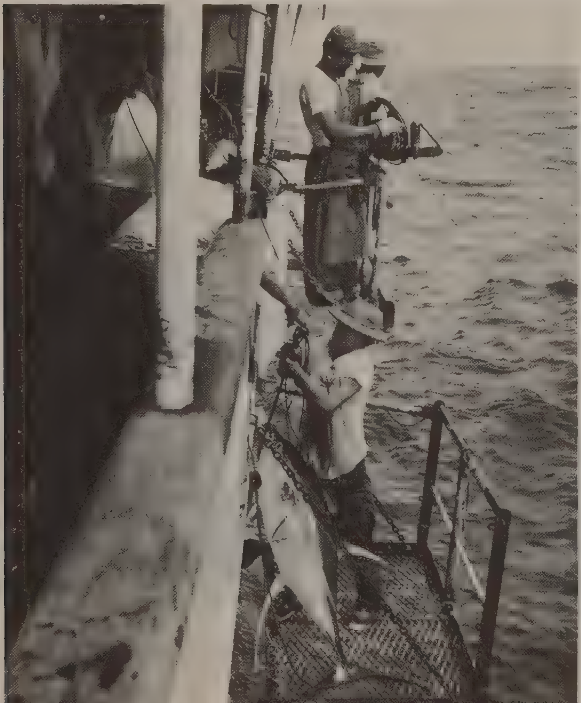

Fig. 5. Hoisting a Yellowfin Tuna Through the Bulwark Gate (Note Line-Hauling Operation in the Background)

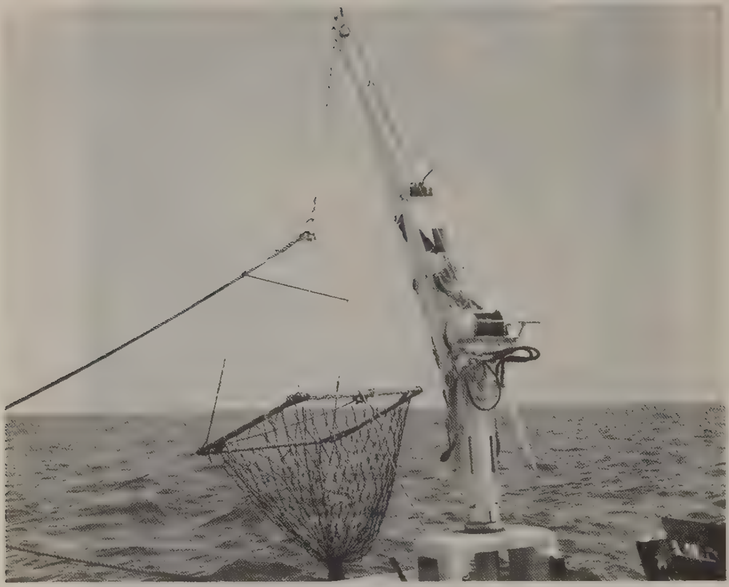

Fig. 6. Rectangular Net Used to Land Large Fish Caught on R/V Anton Bruun Cruise 5

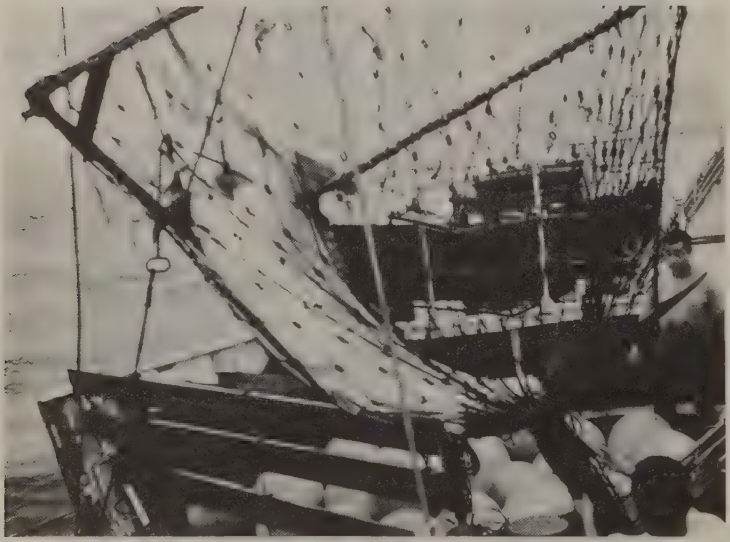

Fig. 7. Landing a 229-kg Black Marlin with the Rectangular Net

FAO Fisheries Reports, No. 54 FR/R54

Report of the IPFC Group of Experts on the Indian Ocean

THE PRESENT STATUS OF FISHERIES AND ASSESSMENT OF POTENTIAL RESOURCES OF THE INDIAN OCEAN AND ADJACENT SEAS

By

R.S. Shomura, D. Menasveta, A. Suda and F. Talbot

Rome, 23-25 January 1967

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

Rome, December 1967

PREPARATION OF THIS REPORT

This is the third version of a report prepared by the Group of Experts on the Indian Ocean established by the Twelfth Session of the Indo-Pacific Fisheries Council (IPFC), Honolulu, Hawaii, U.S.A., October, 1966. The Group of Experts is an advisory body to the Committee on Fisheries or any other body concerned with programming and co-ordination of fishery investigations in the Indian Ocean. Its members are: Mr. R.S. Shomura, Convenor (U.S.A.), Dr. D. Menasveta (Thailand), Dr. A. Suda (Japan), and Dr. F. Talbot (Australia).

The Group held its first meeting in FAO, Rome, in January 1967 to advise the Committee on Fisheries Working Party on the Rational Utilization of the Fishery Resources of the Indian Ocean which considered the first version of this report, issued as working paper COFI:I/1/67/9. It was subsequently revised and reissued in April 1967 under the same symbol as a document of the Second Session of the Committee on Fisheries.

It describes the general oceanographic features of the Indian Ocean and adjacent seas, the pelagic fisheries and the coastal fisheries and suggests areas of potential resource expansion.

The views expressed in this report are those of the authors and not necessarily those of the Food and Agriculture Organization of the United Nations.

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CONTENTS

Page

1. INTRODUCTION 1

2. OCEANOGRAPHY 2

3. PELAGIC FISHERIES 4

    3.1 Development of longline fishery 4

    3.2 Catch and effort data by years 6

    3.3 Yellowfin tuna 6

    3.4 Bigeye tuna 9

    3.5 Albacore 12

    3.6 Southern bluefin tuna 12

    3.7 Marlins 14

    3.8 General needs for future studies 14

    3.9 Latent resources 17

4. COASTAL FISHERIES 17

    4.1 Introductory note 17

    4.2 Brief summaries of the stocks and potential increases in production in different coastal areas 18

    4.3 Inadequacy of statistics from coastal waters 28

    4.4 Coastal areas and resources of the Indian Ocean requiring attention 28

5. LITERATURE CITED 31

1. INTRODUCTION

Of the three major oceans, the Indian Ocean and its adjacent seas rank last in terms of contribution to world production of marine foodstuffs. In 1964 the production of the oceans and their adjacent areas was 25.4 million metric tons for the Pacific, 18.1 million metric tons for the Atlantic, and only 2.0 million metric tons for the Indian Ocean (FAO, 1967). Although this difference could be explained on the basis that the total area of the Indian Ocean and adjacent seas is considerably less than that of either the Atlantic or Pacific Oceans, a rough adjustment for these areal differences still shows a low yield from the Indian Ocean.

In 1964 the average yield in metric tons per km^2 for the oceans and their adjacent areas was roughly 0.17 for the Atlantic, 0.14 for the Pacific, and 0.03 for the Indian Ocean (Table 1). These results suggest either that the conditions in the Indian Ocean are drastically different from those in the other two oceans and therefore support smaller amounts of fishery resources, or that the Indian Ocean and its adjacent seas are not being fished to their maximum potential. If the latter is true, the Indian Ocean contains vast latent or underutilized resources.

TABLE 1. Comparison of marine catch of the three major oceans and their adjacent seas

Ocean	Area[1/] (10^6 km^2)	Marine catch for 1964[2/] (million metric tons)	Metric tons per km^2
Atlantic	106.463	18.1	0.17
Pacific	179.679	25.4	0.14
Indian	74.917	2.0	0.03

[1/] From Sverdrup, Johnson, and Fleming (1946).

[2/] From FAO (1967).

One difference between the oceans is the presence of temperate areas in the Atlantic and Pacific Oceans which support large fisheries, and the lack of equivalent temperate areas in the Indian Ocean. The presence of rich fisheries within tropical latitudes off Peru as a result of upwelling indicates, nevertheless, that great yields need not necessarily come from temperate climates. Although conceivable, it is highly unlikely that the low production in the Indian Ocean results from basic shortcomings in the physical and chemical makeup of the Indian Ocean. On the contrary, there is evidence that productivity in some areas of the Indian Ocean equals or exceeds that of the most productive areas of other oceans. Ryther and Menzel (1965), who used the C_{14} method to determine carbon assimilation, obtained rates of productivity of 5.7 and 6.4 g carbon/m^2/day for two stations off the Gulf of Oman. They indicated that these values were "...higher than ever before reported for the ocean." Furthermore, the average rate for 30 stations in the Arabian Seas was 1.8 g carbon/m^2/day, a value considerably higher than the average for oceanic waters.

If productivity is similar in the three oceans, the yield of marine resources in the Indian Ocean would have to be increased fourfold to sixfold to bring it to a level comparable to that of the Atlantic and Pacific. This potential level may be minimal, since there is some evidence that the maximum yields for the Atlantic and Pacific Oceans have not yet been attained.

The pelagic longline fishery is operationally the same in all the oceans, but striking differences are evident when one compares the coastal fisheries of the Indian Ocean with those of the Atlantic and Pacific. First, although there are many individual fisheries in the Indian Ocean, they are all very small. Second, they depend on the use of gear of relatively low efficiency. Whereas the fisheries in the other oceans use highly mechanized boats (e.g., the large stern trawlers of the Grand Banks fishery in the North Atlantic Ocean), the fisheries of the Indian Ocean generally use small craft with little or no mechanized power. Much of the fishing in the coastal waters of the Indian Ocean and adjacent seas is limited to waters near coastal ports. The range is to a large extent limited by the small size of the craft and the general lack of refrigeration.

As we indicate in the present report, the data on the pelagic fisheries suggest that the quantity of pelagic resources now being harvested by the longline technique may be at the upper limit of rational harvesting--and that there is an immediate need for basic data that will permit accurate estimates of the maximum sustainable yields for each of the commercially important species. On the other hand, there is every indication that the coastal resources are underutilized and that there is potential for considerable development and expansion.

We describe here the general oceanographic features of the Indian Ocean and adjacent seas, the pelagic fisheries, and the coastal fisheries, and suggest areas of potential resource expansion.

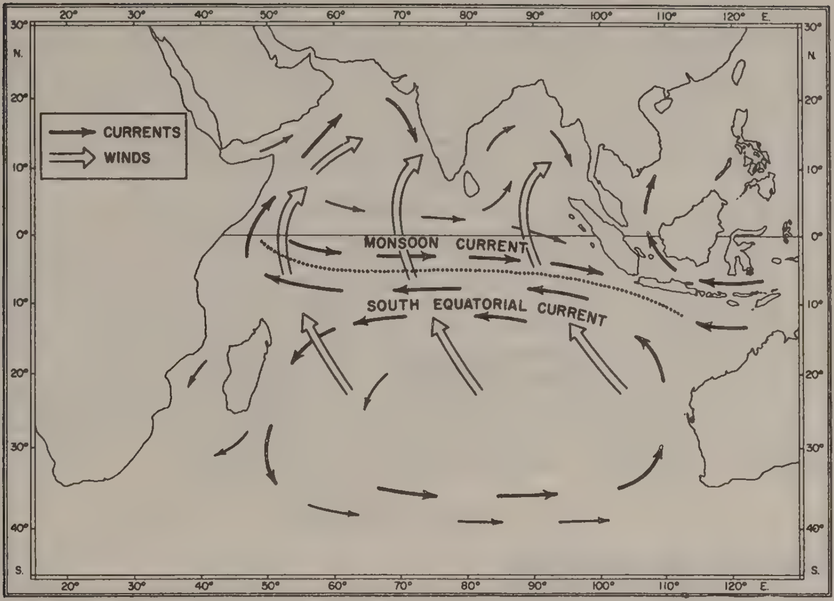
In presenting the data, we have separated the marine resources into two broad categories, namely the pelagic and the coastal fisheries. It should be stressed that a clearcut spatial separation of these two categories is not possible nor desirable. For convenience the principal species included in the pelagic fisheries section are the tunas and billfishes. Although these species occur at various depths in waters a considerable distance from land masses, some species are also commonly caught close to shore and with shore species. Rather than treat these occurrences under the coastal category we consider it essential that our discussions be resource-oriented rather than space-oriented.

2. OCEANOGRAPHY

The dominant features in the circulation of surface waters in the Indian Ocean are the two monsoons. The monsoon periods can be separated into the Northern Hemisphere summer (May-September) and the Northern Hemisphere winter (November-March). In the Southern Hemisphere during May-September, the prevailing winds are from the southeast and are referred to as southeast monsoons. North of the equator, these winds shift direction, owing to the coriolis effect, and are known as the southwest monsoons. During November-March, the winds originate over the Asian continent and blow from a general northeast direction in the Northern Hemisphere, where they are referred to as the northeast monsoon. South of the equator, these winds shift direction, owing to the coriolis effect, and become known as the northwest monsoon.

The most prominent oceanographic feature in the Southern Hemisphere is the major counterclockwise gyre between latitudes 8° S and 40° S (Figs. 1 and 2). The northern limb of this gyre is the South Equatorial Current and the entire system is reported to be fairly well developed throughout the year.

In comparison with the southern sector the circulation of surface waters in the northern part of the Indian Ocean is very complex. During May-September Pacific Ocean water passes into the Indian Ocean through the Timor Sea and Torres Strait between New Guinea and Australia (Fig. 1). This water, along with the northern limb of the counterclockwise gyre of the South Indian Ocean, forms the South Equatorial Current and flows westward towards Africa. At the African coast most of the South Equatorial Current Water moves northward along the east African coast as the East African Coastal or Somali Current. A lesser portion of the South Equatorial Current is deflected by Madagascar southwards to form the Agulhas Current. The surface monsoon currents in the Arabian Sea and the Bay of Bengal generally move clockwise. The easterly flowing countercurrent is present throughout the year; during May-September, the axis is at the equator.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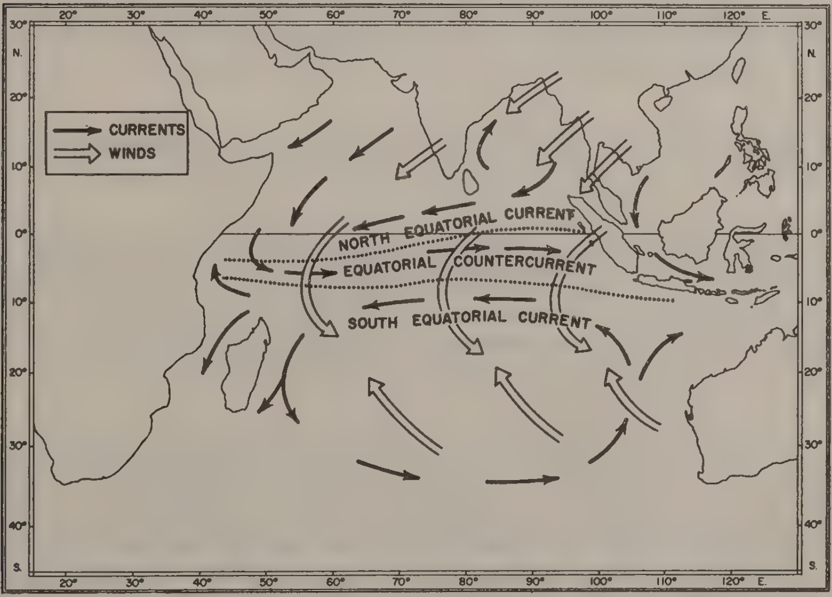
S.

Figure 1. Wind and surface water circulation during the Northern Hemisphere summer period. (From unpublished report by F.S. Osell, U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.)


CURRENTS
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NORTH EQUATORIAL CURRENT
EQUATORIAL COUNTERCURRENT
SOUTH EQUATORIAL CURRENT
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N.
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0°
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20°
30°
40°
S.

Figure 2. Wind and surface water circulation during the Northern Hemisphere winter period. (From unpublished report by F.S. Osell, U.S. Bureau of Commercial Fisheries Biological Laboratory.)

During the Northern Hemisphere winter, the circulation in the southern part of the Indian Ocean is essentially the same as during the Northern Hemisphere summer (Fig. 2). The core of the Equatorial Countercurrent, however, is displaced to the south and in February lies at approximately latitude 8° S. During this season the easterly flowing current noted in the Northern Hemisphere summer is absent and the surface flow is in general westerly. Thus, the westerly flowing North Equatorial Current exists only during the Northern Hemisphere winter when the prevailing winds are from the northeast.

The foregoing describes in the most general terms the circulation of the surface waters of the Indian Ocean and adjacent seas. Data on the formation of water masses and water types and their areal and temporal distributions are vital in the understanding of marine resources; however, the complexity of the subject precludes a detailed statement in the present summary report. It should be pointed out, however, that a proper appreciation of the influence and effects of the environment on the populations of organisms in the sea requires detailed information on the time and space distributions of water masses, water types and upwellings. Undoubtedly, the tremendous fluctuations in the landings of some coastal fishes, e.g. the oil sardine (Sardinella longiceps) of the west coast of India, are influenced by the year-to-year variations in the physical and chemical environment. Nakamura, Yabuta, and Mimura (1958) suggested a close association between the distribution of pelagic fishes and the major current systems.

3. PELAGIC FISHERIES

3.1 Development of longline fishery

Before the entrance of Japanese commercial longline fishing boats into the eastern Indian Ocean waters in 1952, there was a general lack of knowledge of the distribution and abundance of commercially important pelagic fish species in the Indian Ocean--notably the tunas and billfishes. The pelagic fisheries existing before 1952 were in reality coastal fisheries that harvested species generally considered pelagic in habitat. Included in these so-called pelagic fisheries are the pole-and-line fishery for skipjack tuna (Katsuwonus pelamis) which operates from the island of Minicoy in the Maldive Island group, the handline fishery for yellowfin tuna (Thunnus albacares) in the Gulf of Aden, and the fishery for Euthynnus affinis and longtail tuna (Thunnus tonggol) along the southwest coast of India.

Without including the tunalike scombriform species, e.g. Acanthocybium, it is doubtful that the catch of tunas in the Indian Ocean before 1952 exceeded 10,000 metric tons. Indeed, it is more likely that the landings were around 5,000 metric tons.

The first indication of the existence of a pelagic fishery resource in the Indian Ocean was provided by Japanese exploratory longline fishing cruises conducted before World War II (Kataoka, 1957). In 1930 the exploratory fishing vessel, Shirotaka Maru, fished with longline gear off Andaman and Nicobar Islands in the Bay of Bengal and off the Maldive Islands in the central Indian Ocean. During the early 1930's the Japanese research ship, Haruna Maru, fished off Java and Sumatra. The catches made by these two vessels gave the first indication that commercial quantities of yellowfin tuna and various species of billfishes existed in the Indian Ocean.

In October 1952 the Japanese took advantage of this information and began fishing in the eastern Indian Ocean, primarily for yellowfin tuna. The success of this commercial effort led to an intensification in fishing effort in 1953 and started the development of the Indian Ocean pelagic fishery. Figure 3 shows the areal development of the Japanese longline fishery in the Indian Ocean (Kamimura, 1966). By 1956 the fishing fleet had extended operations as far west as the African coast and by 1960 fishing was carried out from about latitude 15° N to latitude 35° S. Presently longline fishing fleets of other nations--Korea, China (Taiwan), and the U.S.S.R.--are also harvesting the pelagic resources of the Indian Ocean.

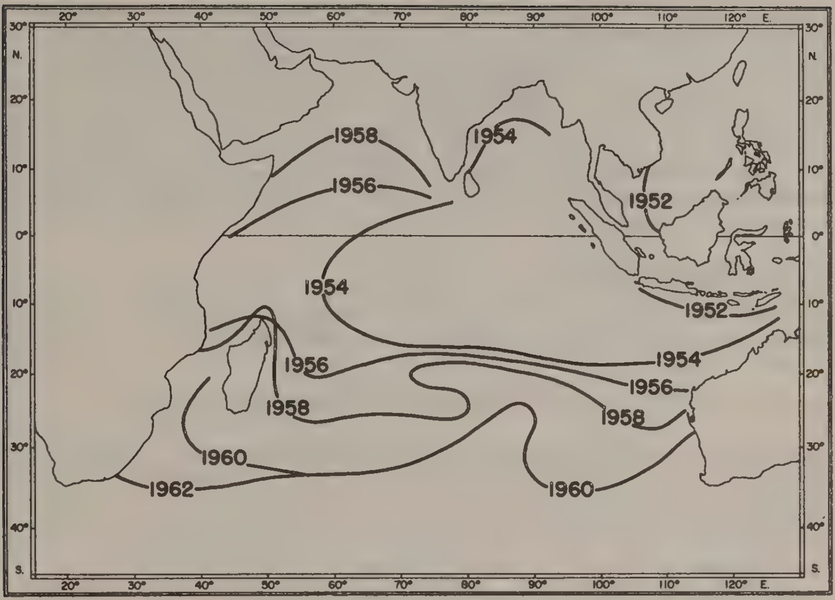
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Figure 3. Development of the Japanese longline fishery in the Indian Ocean and adjacent seas. Heavy lines indicate the outer limits of the fishery in different years.

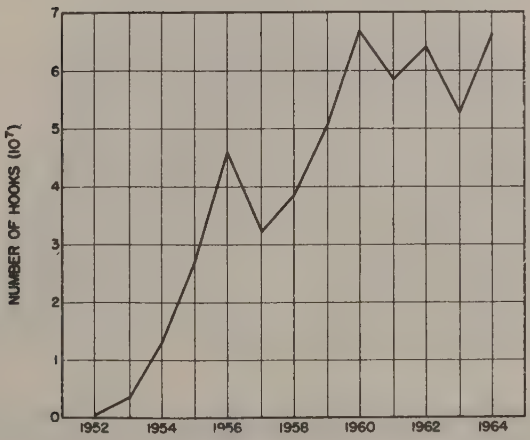


Figure 4.--Estimated Japanese longline fishing effort (hooks) in the Indian Ocean and adjacent seas.

Part of the westward and southward expansion of the fishery was in response to shifts in the principal species sought. In the early years fishing was confined to equatorial waters primarily to catch yellowfin tuna, which then commanded a premium price in the world market. This search for tuna led to the westward expansion of the fishery in equatorial waters. In the middle and late 1950's the decline in yellowfin tuna catch rates and an increased demand for southern bluefin tuna (Thunnus maccoyi) for "sashimi" and fish sausages in Japan led to an increase in effort in the southern bluefin tuna fishing grounds west and northwest of Australia. Finally, the expansion of the fishery in recent years toward the south and southwest was principally to take albacore (Thunnus alalunga) which were encountered in commercial quantities in these sectors.

3.2 Catch and effort data by years

Estimates of the number of hooks fished by Japanese longliners in the Indian Ocean during 1952-64 are shown in Figure 4. Effort increased steadily until 1960 and then leveled at about 60 million hooks per year.

The following should be noted in Figure 5 concerning the annual change in catch:

1. The high catch of yellowfin tuna in 1956 was brought about by the rapid expansion of the fishery into new grounds which contained large virgin stocks. The 1962 high is attributable to the presence of a large year class and the resultant concentration of fishing effort.

2. The increase in southern bluefin tuna catch in 1959 resulted from an expansion of the fishery to the new grounds located south of the previously exploited grounds northwest of Australia.

3. The catch of albacore also shows a gradual increase from 1952. This increase was caused by the southward expansion of the fishery into good concentrations of albacore discovered in the western part of the Indian Ocean.

3.3 Yellowfin tuna

3.3.1 Distribution. Yellowfin tuna are tropical in habitat and the greatest concentrations are in equatorial waters (Fig. 6). This species is taken in varying amounts throughout the southern areas fished, but is virtually absent in the northern waters of the Arabian Sea and the Bay of Bengal.

3.3.2 Availability and abundance. The annual changes in abundance and the number of hooks are shown in Figure 7. The decline in hooking rate indicates the reduction in population by fishing. The average size of yellowfin tuna taken by longline gear has reportedly decreased since the start of the fishery (Mimura, 1958).

3.3.3 Spawning and maturation. A study of gonad development indicates that spawning occurs throughout tropical waters nearly year-round (Figs. 8a and 8b). The distribution of yellowfin tuna larvae is shown in Figure 9. Although the available data are few, the larval distribution tends to coincide with the areas of peak gonad development.

3.3.4 Subpopulations and migration. No evidence of the existence of subpopulations is available. Mimura (1958) suggested that yellowfin tuna migration in the Indian Ocean is not extensive, since high catch rates were attained in each newly exploited area. This condition would not have existed if fishing pressure was being exerted on a single highly mobile population.

3.3.5 Population dynamics and stock assessment. Some estimates of the coefficient of natural and fishing mortalities have been computed for yellowfin tuna in the Indian Ocean (Kawakami and Kitahara, 1964; Hayashi, 1966). The relative abundance of young (3-year-old)

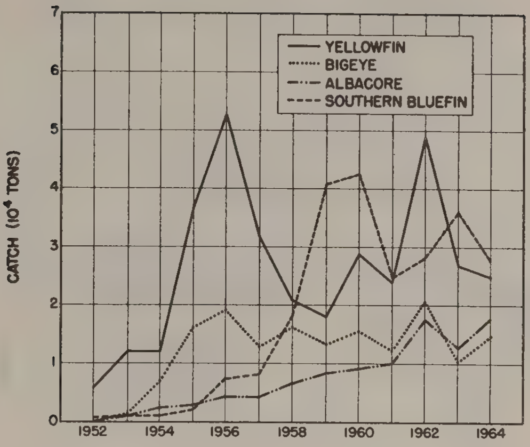
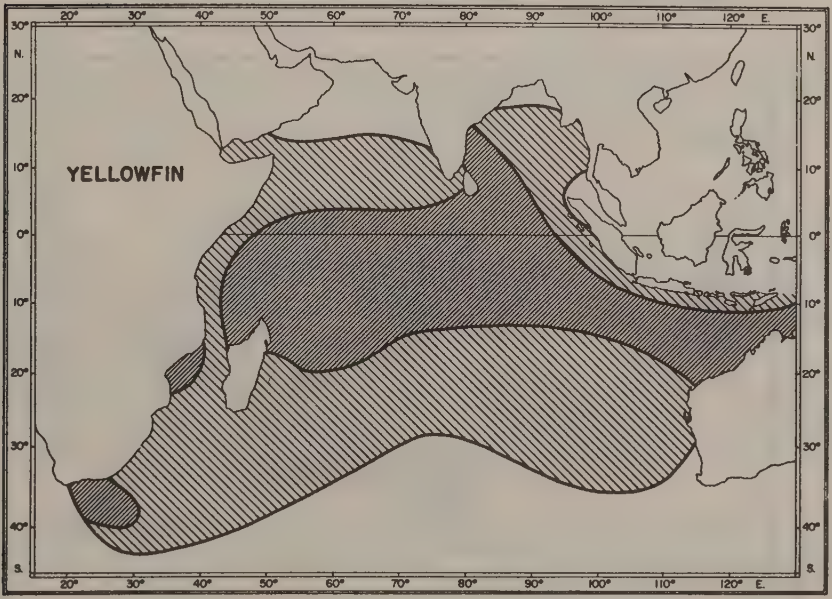


Figure 5. Estimated total tuna catch by the Japanese longline fishery in the Indian Ocean and adjacent seas.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40°
50°
60°
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80°
90°
100°
110°
120° E.
30° N.
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0°
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20°
30°
40°
S.

Figure 6. Distribution of yellowfin tuna in the Indian Ocean and adjacent seas. (Darker areas denote greater concentrations.)

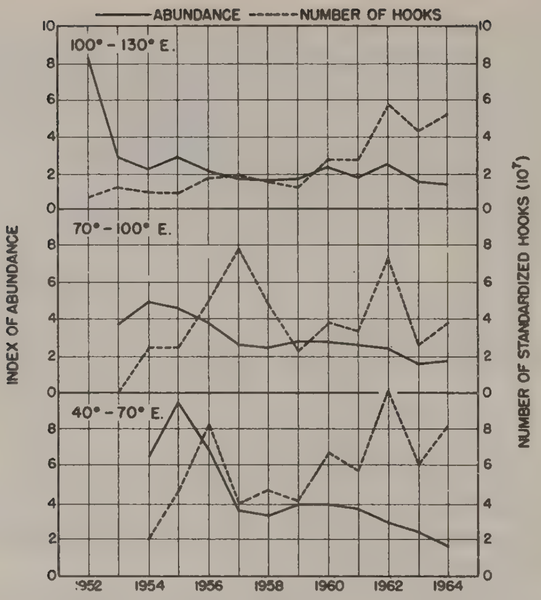
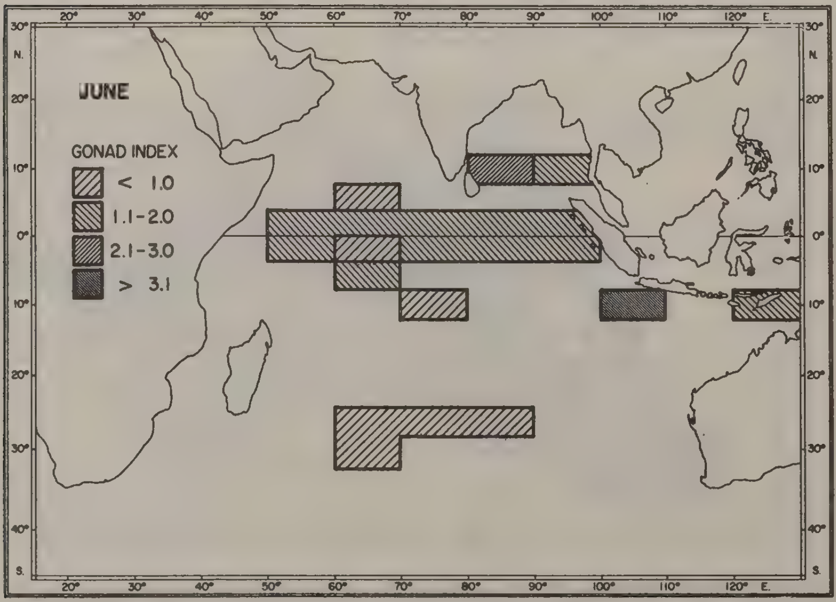


Figure 7. Annual changes in relative abundance of yellowfin tuna and fishing effort, 1952-64. (Index of abundance and standardized hooks reflect adjustments for non-random distribution of species and of fishing effort.)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100°
110°
120° E.
30° N.
20°
10°
0°
10°
20°
30°
40°
S.

Figure 8a. Maturation of yellowfin tuna in the Indian Ocean and adjacent seas in June.

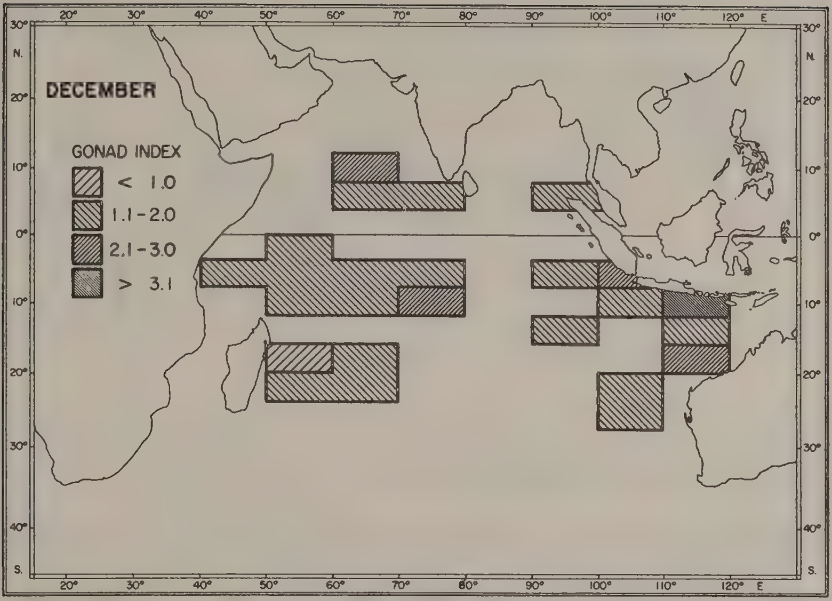

Figure 8b. Maturation of yellowfin tuna in the Indian Ocean and adjacent seas in December. (For key to gonad index, see Figure 8a.)

fish has not shown a noticeable decrease with increasing fishing effort, which suggests that recruitment is being maintained. Hayashi (1966), on the basis of catch and effort data, suggested that the present fishing intensity may be very close to the maximum level for rational utilization of this species in the Indian Ocean.

3.4 Bigeye tuna

3.4.1 Distribution. Bigeye tuna are taken throughout the longline fishing grounds in the Indian Ocean (Fig. 10). In tropical waters the greatest concentrations appear to be between the equator and latitude 10° S in the eastern Indian Ocean and between the equator and latitude 10° N in the western Indian Ocean. At higher latitudes, relatively good bigeye tuna catches have been made in waters off South Africa.

3.4.2 Availability and abundance (Fig. 11). Sakamoto (1966) recently analyzed catch and effort data and concluded that the population of bigeye tuna has decreased in the Indian Ocean since the start of the fishery. The rate of decrease, however, is considered small. The abundance of fish over 5 years old declined dramatically as a result of fishing the accumulated stocks. The abundance of 2-, 3-, and 4-year-olds has leveled off.

3.4.3 Maturation and spawning. Spawning takes place in the same areas as that of the yellowfin tuna. On the basis of gonad studies (Kikawa, 1966), spawning is said to occur throughout the year. Very little is known about the occurrence of larval and juvenile bigeye tuna in the Indian Ocean.

3.4.4 Subpopulations and migration. A suggestion of an east-west migration is indicated by the areal shifts in bigeye tuna concentrations (H. Sakamoto, unpublished data).

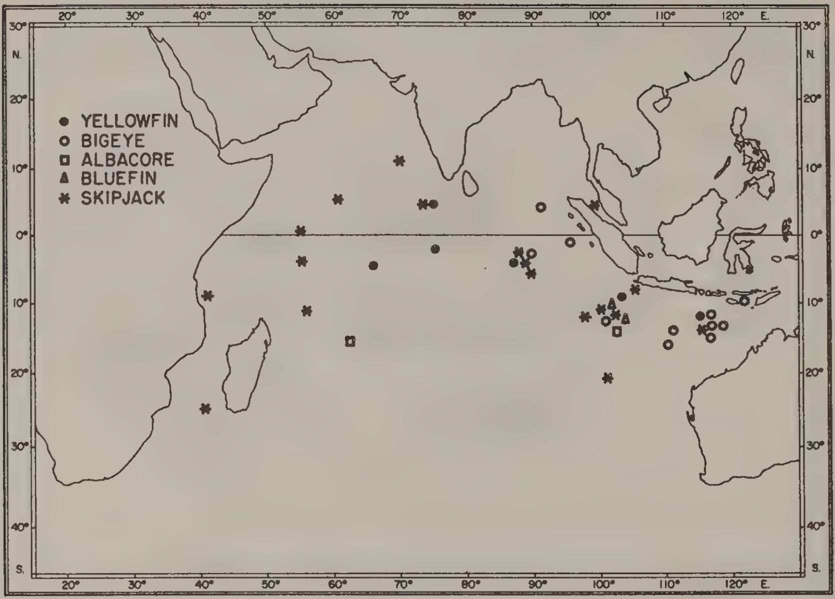
● YELLOWFIN
○ BIGEYE
□ ALBACORE
▲ BLUEFIN
✱ SKIPJACK
20° 30° 40° 50° 60° 70° 80° 90° 100° 110° 120° E.
30° N. 20° 10° 0° 10° 20° 30° 40° S.

Figure 9. Distribution of tuna larvae in the Indian Ocean and adjacent seas.

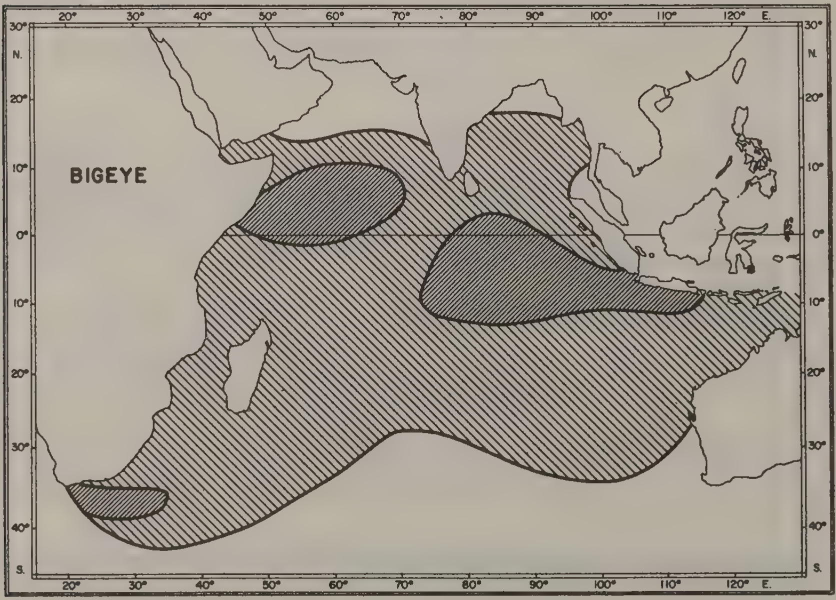
BIGEYE
20° 30° 40° 50° 60° 70° 80° 90° 100° 110° 120° E.
30° N. 20° 10° 0° 10° 20° 30° 40° S.

Figure 10. Distribution of bigeye tuna in the Indian Ocean and adjacent seas.
(Darker areas denote greater concentrations.)

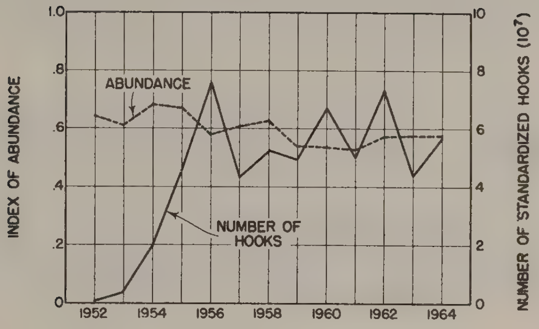

Figure 11. Annual changes in relative abundance of bigeye tuna and fishing effort, 1952-64. (Index of abundance and standardized hooks reflect adjustments for non-random distribution of species and of fishing effort.)

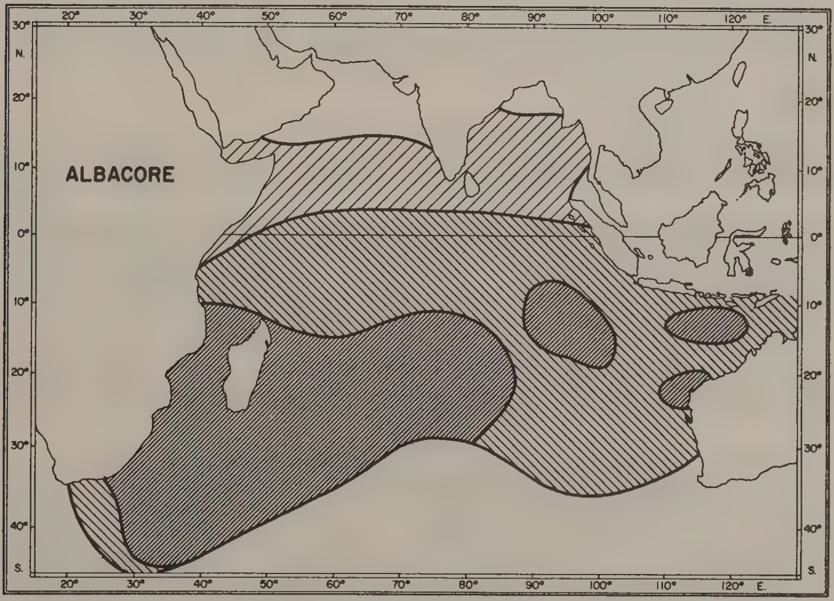
ALBACORE
20°
30°
40°
50°
60°
70°
80°
90°
100°
110°
120° E.
30° N.
20°
10°
0°
10°
20°
30°
40° S.

Figure 12. Distribution of albacore in the Indian Ocean and adjacent seas. (Darker areas denote greater concentrations.)

3.4.5 Population dynamics and stock assessment. Suda (1966) computed the coefficient of natural mortality for bigeye tuna to be approximately 0.6. The fishing mortality coefficient fluctuated between 0.3 and 0.6; the higher value was in 1956. Suda (1966) concluded that the maximum sustainable yield of bigeye tuna would be achieved at a fishing mortality coefficient of 0.7.

3.5 Albacore

3.5.1 Distribution. In the Indian Ocean and adjacent seas the albacore is virtually absent north of the equator (Fig. 12). The greatest density is in the southwest sector of the Indian Ocean.

3.5.2 Availability and abundance. A remarkable increase in fishing effort in 1962 resulted from the southern expansion of the fishing grounds into the western Indian Ocean (Fig. 13). The relative abundance of albacore gradually decreased after 1953, and in 1963 was about half that of the earlier years.

3.5.3 Maturation and spawning. Albacore with well-developed ova were caught in an area in the western Indian Ocean roughly bounded by latitudes 10° S and 30° S (Kikawa and Ferraro, in press). Detailed data are not available on albacore spawning in the Indian Ocean. Information on occurrence and distribution of larval and juvenile albacore is also lacking.

3.5.4 Subpopulations and migration. Marr and Sprague (1963), on the basis of albacore blood group frequency data published by Suzuki, Morio, and Mimoto (1959), concluded that the Indian Ocean sample was a mixture of two or more subpopulations. No evidence is available on the existence or extent of intermingling of Indian Ocean albacore with albacore from the Pacific and Atlantic Oceans.

3.5.5 Population dynamics and stock assessment. No information is available.

3.6 Southern bluefin tuna

3.6.1 Distribution. Southern bluefin tuna are taken in abundance northwest, west, and southeast of Australia (Fig. 14). This species is also reported to be present in large numbers off South Africa during the Southern Hemisphere winter (Talbot and Penrith, 1963).

3.6.2 Availability and abundance. A substantial increase in catch of southern bluefin tuna off the Australian coast was brought about by increased effort by the Australian pole-and-line fishery. The average level of abundance (1958-64) of the southern bluefin tuna is now about one-third of the level of the earlier years. The abundance of fish older than 8 years has decreased drastically, especially since 1962.

3.6.3 Maturation and spawning. Spawning has been reported to occur in tropical waters northwest of Australia from September to March, with a peak in November (Mimura and Warashina, 1962).

3.6.4 Subpopulations and migration. C. Shingu (unpublished manuscript) developed a model of the migration of southern bluefin tuna in the Indian Ocean (Fig. 15). On the basis of the model, southern bluefin tuna spawn northwest of Australia. The young move southward and eastward along the Australian coast. Fairly extensive movement of small southern bluefin tuna in south Australian waters has been demonstrated by tag recoveries (Robins, 1963). Return of large, maturing southern bluefin tuna to the spawning grounds is postulated to occur in the offshore waters south of Australia.

3.6.5 Population dynamics and stock assessment. The Australian and Japanese catch of 1.5 million southern bluefin tuna has been estimated to represent about 10 percent of the population of southern bluefin tuna off South Australia (Hynd, Kesteven, and Robins, 1966).

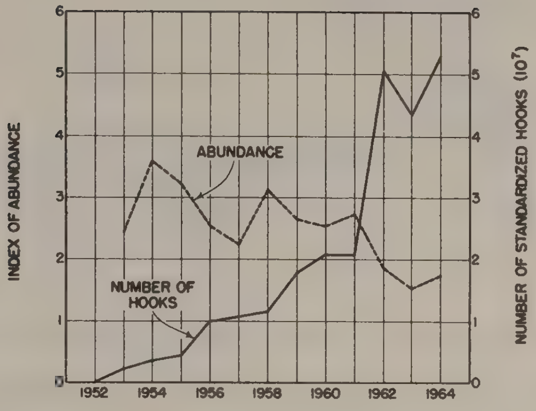

Figure 13. Annual changes in relative abundance of albacore and fishing effort, 1952-64. (*Index of abundance* and *standardized hooks* reflect adjustments for non-random distribution of species and of fishing effort.)

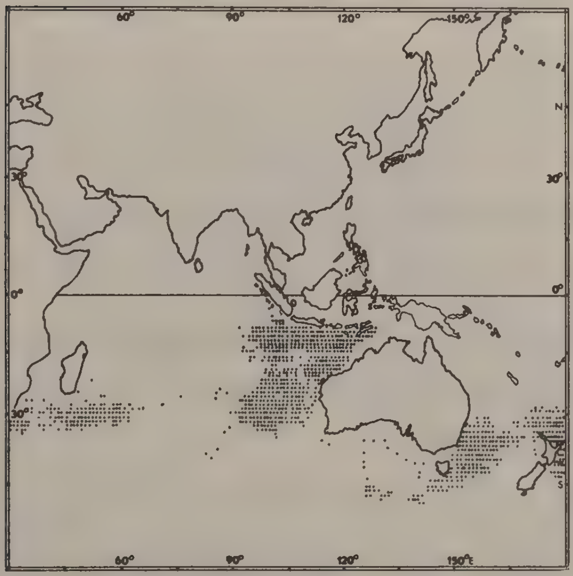

Figure 14. Distribution of southern bluefin tuna in the Indian Ocean and adjacent seas. (Stippling denotes recent catches by longline.)

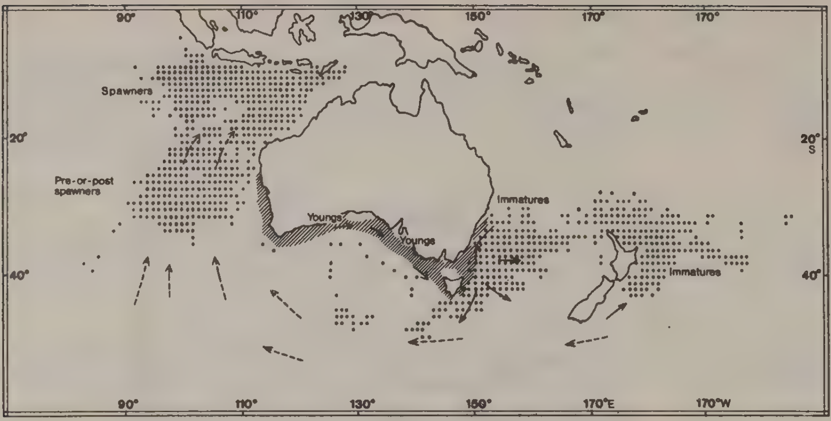

Figure 15. Migratory routes of the southern bluefin tuna off Australia and New Zealand. Stippling denotes catches by longline. (From an unpublished manuscript by C. Shingu, Nankai Regional Fisheries Research Laboratory, Kochi, Japan.)

Figure 16 shows the yield-per-recruit relationship for bluefin tuna computed by Hayashi (1966). The relationship was determined from data from the pole-and-line fishery in coastal waters as well as the longline fishery in offshore areas. The pronounced decrease in abundance of the advanced age group has been directly attributed to the increase in fishing pressure, and indirectly to the reduced recruitment resulting from increased catch in the longline grounds in the Pacific and the pole-and-line fishery off Australia.

3.7 Marlins

3.7.1 *Distribution*. The distributions of striped marlin (*Tetrapturus audax*), blue marlin (*Makaira nigricans*), and black marlin (*M. indica*) are shown in Figures 17, 18, and 19. Striped marlins are abundant in the Bay of Bengal and along the southern coast of India. The center of abundance of blue marlin appears to be south of the center of abundance of striped marlin. The highest density of black marlin is in the eastern Indian Ocean.

3.7.2 *Availability and abundance*. Changes in availability and abundance have not been determined for the three species of marlins, although some data are available.

3.7.3 *Maturation and spawning*. Spawning takes place in the subtropical and tropical waters.

3.7.4 *Subpopulations and migration*. No information is available.

3.7.5 *Population dynamics and stock assessment*. No information is available.

3.8 General needs for future studies

3.8.1 *Data on catch and effort and size frequency*. Accurate estimates of population abundance require the availability of accurate catch and effort data. The Japanese now have a highly developed sampling program to collect longline data. Even under their sampling system, however, it has been necessary to estimate the total oceanwide catch and effort on the basis of only a small fraction of the fishery that has been sampled. As indicated earlier, other countries--China (Taiwan), Korea, and U.S.S.R.--are now fishing in the pelagic waters of the Indian Ocean. Data on catch and effort from these countries are not readily available.

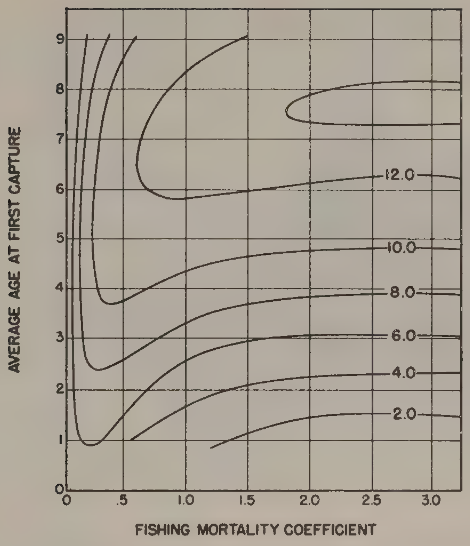

Figure 16. Yield-per-recruit relationship of southern bluefin tuna. (From Hayashi, 1966.)

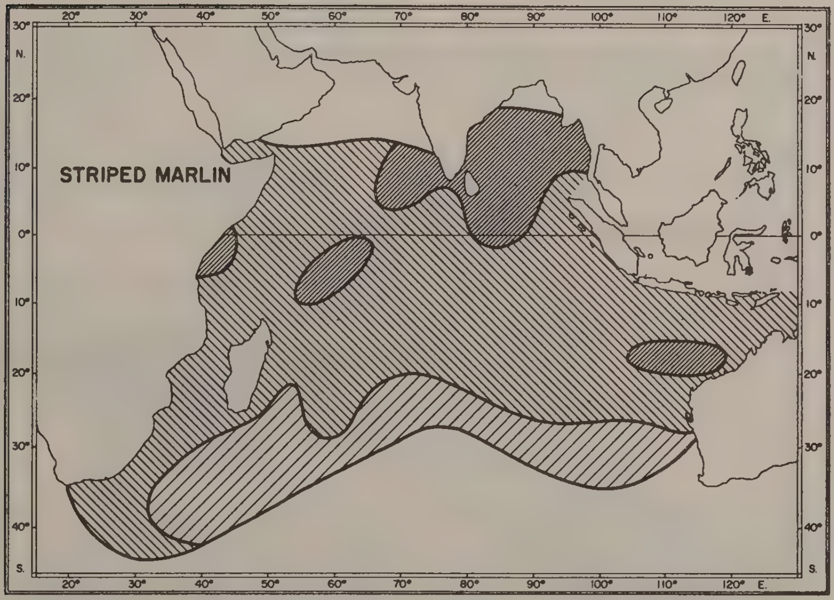
20°
30°
40°
50°
60°
70°
80°
90°
100°
110°
120° E.
30°
N.
20°
10°
0°
10°
20°
30°
40°
S.
STRIPED MARLIN

Figure 17. Distribution of striped marlin in the Indian Ocean and adjacent seas. (Darker areas denote greater concentrations.)

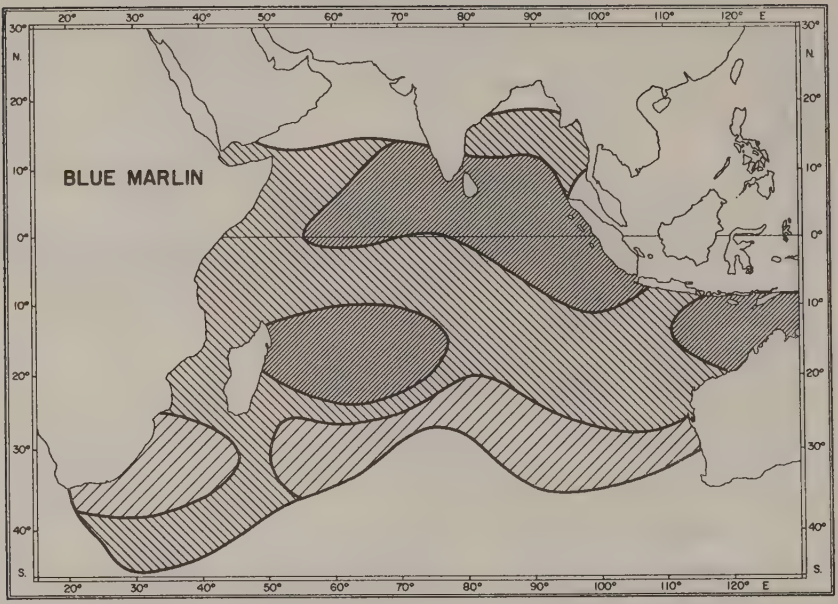
BLUE MARLIN
20° 30° 40° 50° 60° 70° 80° 90° 100° 110° 120° E
30° N. 20° 10° 0° 10° 20° 30° 40° S.

Figure 18. Distribution of blue marlin in the Indian Ocean and adjacent seas. (Darker areas denote greater concentrations.)

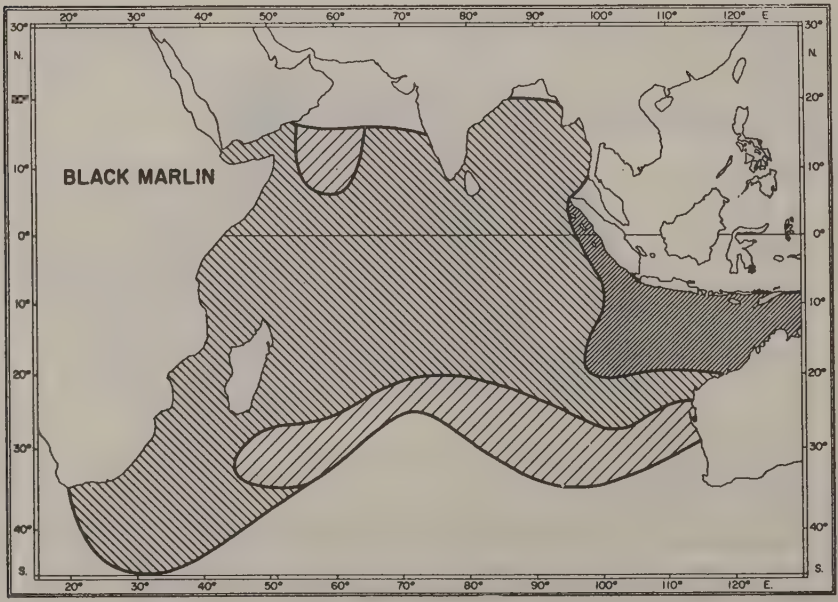
BLACK MARLIN
20° 30° 40° 50° 60° 70° 80° 90° 100° 110° 120° E
30° N. 20° 10° 0° 10° 20° 30° 40° S.

Figure 19. Distribution of black marlin in the Indian Ocean and adjacent seas. (Darker areas denote greater concentrations.)

3.8.2 Subpopulation studies. It is obvious from the discussion of the various species that information on subpopulations is poor or lacking. Because of the importance of subpopulation data for population dynamics studies, it is highly desirable that tagging experiments and morphometric and serological studies be undertaken.

3.9 Latent resources

3.9.1 Skipjack tuna. Although a number of the tuna species in the Indian Ocean are being taken by the longline gear at levels which suggest little or no potential increase, the skipjack tuna gives every indication of being a vast underutilized resource. Presently the principal fisheries for skipjack tuna are the pole-and-line fishery of Minicoy and the small trolling fishery of Ceylon. Complete data on the total skipjack tuna production in the Indian Ocean is lacking; however, even a generous estimate would place the total annual yield at less than 5,000 metric tons. By comparison, the skipjack tuna yield for the Pacific Ocean is about 250,000 metric tons. Even with this sizable landing in the Pacific the resource is considered to be underutilized, especially in the central tropical Pacific. It is highly conceivable that there is also a large resource of skipjack tuna still to be harvested in the Indian Ocean.

3.9.2 Saury. Sauries have been encountered throughout a wide area of the southern Indian Ocean. As with skipjack tuna, the saury may represent a large latent resource.

4. COASTAL FISHERIES

4.1 Introductory note

To facilitate the compilation of information on important coastal fisheries, the coastline of the Indian Ocean has been divided into the following areas (Fig. 20):

1. South Africa (Indian Ocean coast)
2. East African coastal region (Mozambique, Tanzania, and Kenya)
3. Madagascar
4. Western Indian Ocean islands
5. Gulf of Aden and adjacent areas (Somalia, Aden, Southern Arabia)
6. Red Sea and Gulfs of Suez and Aqabar
7. Gulfs of Persia and Oman
8. Coasts of West Pakistan, India, East Pakistan, and Ceylon
9. Coasts of Burma, Thailand, and Malaysia
10. West coast of Indonesia
11. West coast of Australia

The coastal fisheries of most of the countries bordering the Indian Ocean are in general of an undeveloped, subsistence type. Many countries still use nonmotorized boats and traditional types of gear and techniques, and have not experienced the recent advances in gear technology. Fishing is often very short-range and confined to shallow waters close to the coast.

It is perhaps a truism to state that increased production in many parts of Africa and Asia is possible through mechanization of fishing boats and improvement of the efficiency of gear.

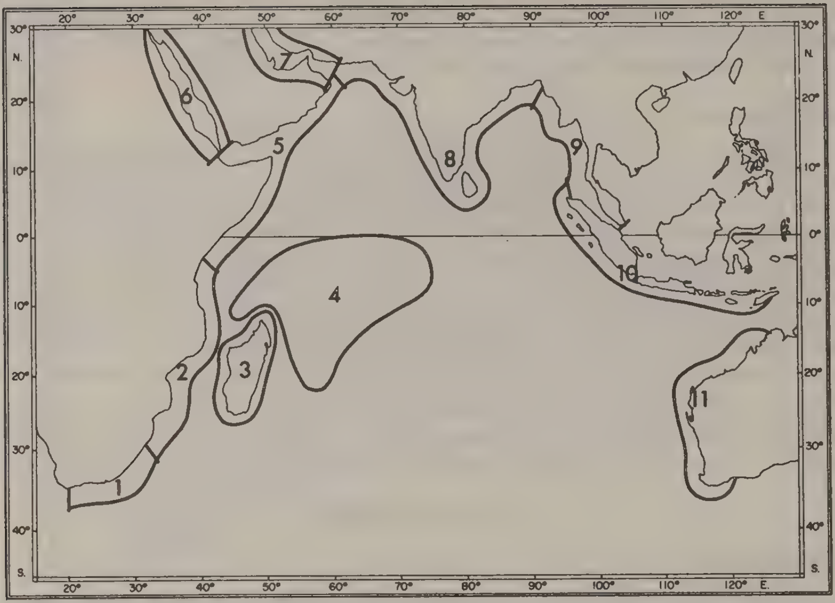

Figure 20. Divisions of coastal and island areas in the Indian Ocean and adjacent seas used in the compilation of available fishery information.

Often, however, the availability of the resource and the catching techniques used are not factors that limit increased production. Production is kept low over much of the Indian Ocean coastal area by other factors, such as availability of storage and distribution facilities at landing areas, fluctuations in supplies and prices of ice, control of prices and catches by powerful middlemen and lack of suitable markets. These controlling factors may be eased by government action.

Panikkar (1966) gave further information on Indian Ocean fisheries.

4.2 Brief summaries of the stocks and potential increases in production in different coastal areas

4.2.1 South Africa (Indian Ocean coast)

4.2.1.1 General description. Coastline with a narrow continental shelf at its northern end widening to the Agulhas Bank (up to 100 miles wide) at the southernmost tip of Africa. The southernmost area is subtropical and the northern tropical. Localized areas of moderately high plankton standing crop, but no major upwelling.

4.2.1.2 Fishing techniques. Trawling with vessels 70 feet long or less, shore seining, handlining from motorized boats, trolling.

4.2.1.3 Species exploited. Flatfish, sciaenids, mugilids, sparids, redfish, seerfish (*Scomberomorus commerson*), sharks, rock lobster (*Palinurus gilchristi*), penaeid prawns (northern coast).

4.2.1.4 Present total production. 3.0 thousand metric tons (Indian Ocean coast).

4.2.1.5 Knowledge of stocks. Species identification good; some information on stock size and migrations of pilchard, and on stock size of flatfish.

4.2.1.6 Possible production increase. No precise information. Some stocks, such as the flatfishes of the Agulhas Bank, are probably not capable of increased production. Others, particularly pilchard (*Sardinops*), and rocky-bottom fishes of the shelf, may be further developed. Increase not likely to be manyfold.

4.2.1.7 Programs for exploration, research, and development. Research investigation into seasonal pilchard run is under way.

4.2.2 East African coastal region (Mozambique, Tanzania and Kenya)

4.2.2.1 General description. Tropical coastline with narrow continental shelf, and without enriched upwelling areas. Typically fringed with mangrove or coral reefs.

4.2.2.2 Fishing techniques. Mostly indigenous fisheries poorly or moderately developed; gear includes handlines, permanent set traps, movable traps, beach seines, set nets, trolling rigs. Some bottom trawling (Mozambique). Some ring netting with lights. Most fishing is without motorized boats, although use of motors is increasing.

4.2.2.3 Species exploited. *Sardinella*, mixed bottom and coral reef fishes, seerfishes (*Scomberomorus commerson*, *S. lineolatus*), sharks, rock lobsters (*Palinurus gilchristi* off southern Mozambique and *Panulirus* spp. in other East African coastal areas), prawns and shrimps (*Penaeus* spp., *Metapenaeus* spp.).

4.2.2.4 Present total production (thousands metric tons). Mozambique, 5.8; Tanzania, 19.2; Kenya, 5.6; total 30.6. Statistics except for Tanzania are not detailed, but bottom fishes probably constitute well over half of this amount, and *Sardinella*, sharks and rays, and seerfishes most of the remainder.

4.2.2.5 Knowledge of stocks. Species identification fair. No information on stock sizes.

4.2.2.6 Possible production increase. Fishery clearly capable of increase. *Sardinella* and other small coastal pelagic fishes little exploited and need attention. Some development of prawn industry possible. In general a twofold, perhaps threefold, increase may be feasible.

4.2.2.7 Programs for exploration, research, and development. Commercial fisheries for shrimp in the Beira area of Mozambique, and for rock lobster (*Palinurus gilchristi*) are being developed.

4.2.3 Madagascar

4.2.3.1 General description. Extensive coastline, with an extremely narrow shelf on its eastern side, and a wider, although not extensive, shelf area on the western coast. Bathed by South Equatorial Current Water, with little enriching except in a small area of upwelling off the southwestern corner.

4.2.3.2 Fishing techniques. In general a subsistence-level fishery with handlines, set nets, and traps. Trolling for seerfishes (*Scomberomorus commerson*), trapping for rock lobster (*Panulirus* spp.), and trawling for prawns are moderately developed.

4.2.3.3 Species exploited. General bottom fishes, seerfishes, rock lobster (*Panulirus* spp.), prawns (*Penaeus* spp., *Metapenaeus* spp.).

4.2.3.4 Present total production. Total production estimated at 5.8 thousand metric tons, with no separation into groups.

4.2.3.5 Knowledge of stocks. Classification of species not well known. No details of stock assessment known. For hydrographic reasons the area would not seem to hold promise of rich fish stocks although the extensive mangrove areas of the Mozambique Channel coast indicate sizable prawn and crab stocks.

4.2.3.6 Possible production increase. No precise information. The sparse population and small number of fishermen would suggest that a manyfold, probably fivefold or more, increase over the 5.8 thousand metric tons is possible. Possibilities of exploitation of Sardinella and associated species on the northwest coast are good.

4.2.3.7 Programs for exploration, research, and development. Research and fishery development are under way on the prawn fishery of the northwest coast. Exploration of the possibilities of a Sardinella fishery on the northwest coast is necessary. Improvement of gear and techniques and use of motorized boats necessary.

4.2.4 Western Indian Ocean islands (Comoro, Mauritius, Reunion, Seychelles, Chagos,...)

4.2.4.1 General description. Scattered tropical islands and banks of both volcanic and coral reef type, stretching over the central and western Indian Ocean. Many are small islands on extensive banks. Fish stocks are those typical of coral reef communities.

4.2.4.2 Fishing techniques. Gear includes handlines, trolling rigs, traps. Motorized boats sometimes used for long-distance fisheries.

4.2.4.3 Species exploited. General coral community bottom fishes, sharks, seerfishes, trevallies.

4.2.4.3 Present total production (thousands of metric tons). Comoro, 1.3; Mauritius, 1.3; Reunion, 2.2; Seychelles, 1.5; total 6.3.

4.2.4.4 Knowledge of stocks. Species identification fair. No stock assessments have been made. Catches off Mauritius are dropping; this area seems badly overfished.

4.2.4.5 Possible production increase. On the basis of exploratory fishing Wheeler (1953) estimated a potential annual demersal fish catch of 2.8 million metric tons for this area. This estimate is greater than the whole Indian Ocean catch reported for 1964. Even if this estimate is much exaggerated, it is probable that this area, which now produces less than 10 thousand metric tons, is badly under-exploited and could be expanded to at least 10 times its current production.

4.2.4.6 Programs for exploration, research, and development. Development under way of a firm based on Mauritius, equipped with freezers, to fish banks. The area needs further survey to confirm Wheeler's potential yield figures.

4.2.5 Gulf of Aden and adjacent areas (Somalia, Aden, South Arabia)

4.2.5.1 General description. This area comprises the tropical East African coastline north of the equator, the Gulf of Aden, and the South Arabian coastline--areas where major upwelling occurs when the southwest monsoon prevails. This upwelling results in primary productivity as high as that in the rich waters off Peru.

4.2.5.2 Fishing techniques. Gear included trolling rigs, handlines, shark nets, ring nets, longlines, and trawls by outside countries, beach seines.

4.2.5.3 Species exploited. Sharks and skates, tuna, seerfish (Scomberomorus commerson), Sardinella and associated species, percomorph bottom fishes.

TABLE 2. Landings of commercially important fish and crustaceans in India, 1959-64[1]

Species or group	Landings in metric tons (average for 1959-64)
Oil sardine (Sardinella longiceps)	145,736
Bombay duck (Harpodon nehereus)	91,911
Prawns and shrimps	68,267
Indian mackerel (Rastrelliger spp.)	67,714
Elasmobranchs	37,549
Other sardines (Sardinella spp.)	33,217
Sciaenids	27,014
White baits (Anchoviella spp.)	24,694
Carangids (Decapterus spp., Megalaspis, Selaroides, and Caranx spp.)	22,794
Ribbonfishes (Trichiurus spp.)	20,780
Silverbellies (Leiognathus spp.)	20,285
Pomfrets (Pampus spp. and Parastromateus niger)	20,170
Catfishes (Tachysurus spp. and Osteogeniosus spp.)	19,118
Big-jawed jumper (Lactarius lactarius)	10,917
Seerfishes (Scomberomorus spp.)	9,650
Eels (Muraenesox spp.)	7,462
Wolf herrings (Chirocentrus spp.)	7,235
Tunnies	4,666
Threadfins (Polydactylus, Polynemus, Eleutheronema spp.)	4,387
Grey mullets (Mugil spp., Liza spp., Valamugil, and Rhinomugil spp.)	1,215

[1] Data from Jones (in press).

4.2.5.4 Present total production (thousands of metric tons). South Arabia, 52.0; Somalia, 4.5; total 56.5

4.2.5.5 Knowledge of stocks. Species identification poor. No data for stock assessment.

4.2.5.6 Possible production increase. Productivity values suggest a fishery potential richer for this area than for any other in the western Indian Ocean. M.B. Schaefer (personal communication) estimated a production as high as 10 million metric tons, or 200 times the present catch. It is likely that this would be mainly of Sardinella and other small inshore pelagic species. Without further estimates of primary production along the whole coastline and over the annual cycle, and some sampling of the fish population, such figures must be treated with caution. Even if the estimates are optimistic, however, this area has enormous potential.

4.2.5.7 Programs for exploration, research, and development. Special fund project (UK 38). Survey of the fishery resources of the Gulf of Aden.

4.2.6 Red Sea and Gulfs of Suez and Aqabar (Ethiopia, Sudan, United Arab Republic, Israel, Jordan, Saudi Arabia, Yemen)

4.2.6.1 General description. The coastal waters of this narrow sea are bounded by coral reefs. Wide shelfs exist only at the southern end of the Red Sea, on the Yemen and Ethiopian coasts. Hydrographically the Red Sea may be considered moderately productive.

4.2.6.2 Fishing techniques. Over most of the area traditional gear is in use, including traps and pots, handlines, trolling lines, set nets and seines, and nonmotorized boats. Although some bordering countries (e.g., Israel) have larger vessels, these are generally used outside the Red Sea.

4.2.6.3 Species exploited. Demersal coral reef species, sharks and rays, herrings, sardines and anchovies, seerfishes and trevallies.

4.2.6.4 Present total production (thousands of metric tons). U.A.R., 9.8; Sudan, 1.6; Ethiopia, 8.9; Saudi Arabia, 6.0; Jordan, 0.2; Israel, 1.3; Yemen, 2.5; total 30.3.

4.2.6.5 Knowledge of stocks. Classification of species moderately well known. No stock assessment figures available.

4.2.6.6 Possible production increase. Unknown. Various fishery experts consider further exploitation possible for sardines, bottom fish, and other coastal fishes (El Sabv and Farina, 1954; Ferrer, 1958; Oswald, 1958).

4.2.6.7 Programs of exploration, research, and development. Request submitted by Jordan for special fund project on fisheries. Improvement of techniques and gear, and motorizing of local boats necessary.

4.2.7 Gulfs of Persia and Oman (Oman, Trucial Oman, Saudi Arabia, Kuwait, Iraq, Iran, Qatar)

4.2.7.1 General description. The Persian Gulf is extremely shallow--under 15 fathoms in average depth and 30 fathoms in maximum depth. Muddy areas near the deltas and sand and coral reefs along much of the shore. The junction between the Persian and Oman Gulfs is shallow, but the Gulf of Oman is 1,500 fathoms deep for half its length. The Gulf of Oman has given extraordinarily rich productivity measures (Ryther and Menzel, 1965).

4.2.7.2 Fishing techniques. The local fisheries are of a subsistence type, without motorized boats; shore seines, gill nets, traps, set traps, handlines and trolling lines are used. Some prawn trawling.

4.2.7.3 Species exploited. Sardines, hilsa, *Stromateus* spp., general coral reef fishes, small tuna and other pelagic scombroids, and trevallies, prawns.

4.2.7.4 Present total production (thousands of metric tons). Oman, 100.0; Trucial Oman, 12.0; Sauda Arabia, 15.0; Kuwait, 6.8; Iraq, 0.5; Iran, 8.0; Qatar, 0.6; total 142.9.

4.2.7.5 Knowledge of stocks. Classification of species poorly known. No stock assessments made.

4.2.7.6 Possible production increase. Not known. Prawns and *Sardinella*-type fishes may be under-exploited.

4.2.7.7 Programs for exploration, research, and development. Prawn trawl fishery being developed. Potential fishery for *Sardinella*-type fishes should be investigated.

4.2.8 Coasts of West Pakistan, India, East Pakistan, and Ceylon

4.2.8.1 General description. The coastal areas of India, Pakistan, and Ceylon are characterized by a long coastline with a prominent shelf along the west coast of Pakistan and the west coast of India. The east coast of India is characterized by a narrow shelf. In the Bay of Bengal the shelf widens to about 120 miles.

The Bay of Bengal receives fresh water from many large rivers; since seasonal precipitation is heavy, the bay has a lower average salinity than the Arabian Sea.

Movement of current along the east and west coasts of India is influenced by the northeast and the southwest monsoons.

The plankton standing crop is higher on the west coast of India than on the east coast. The area is entirely within the tropical zone.

4.2.8.2 Fishing techniques. Fisheries in these areas are more or less on a subsistence level. The fishing gear employed by local fishermen includes bamboo stake traps of various sizes, purse seines, beach seines, gill nets, set bag nets, stake nets, cast nets, and trawl nets.

4.2.8.3 Species exploited. Jones (in press) compiled information on landings fishing gear, and the available biology of the 20 most important species and groups of species of commercial marine fishes (Table 2). His information is based principally on the data from India. Among the 20 species or groups of species listed, three species and three groups of species have landings which are greater than 30.0 thousand metric tons. They are the oil sardine (*Sardinella longiceps*), the Indian mackerel (*Rastrelliger* spp.), the Bombay duck (*Harpodon nehereus*), prawns and shrimps, elasmobranchs, and sardines other than the oil sardine.

4.2.8.4 Present total production. See Table 2 for the average (1959-64) production of various species. Catches in Pakistan and Ceylon combined constitute about one-fourth of the Indian catch.

4.2.8.5 Knowledge of the stocks. Species identification fair. No information is available on the characteristics of the stocks of commercial importance.

4.2.8.6 Possible production increase. No specific information. According to Tiews (in press) trawl fisheries can be expanded in India, Pakistan, and Ceylon. His calculations indicate that it may be possible to harvest about one million metric tons of fish in the available trawling grounds. He estimated the area of these grounds to be about 85,000 square nautical miles.

4.2.8.7 Programs for exploitation, research, and development. Though extensive studies have been made by Indian scientists on the biology (fecundity, stage of maturity, food habits, descriptions of eggs and larvae, ...), only limited studies have been made to determine the causes of the fluctuations in the stocks of these species and population dynamics of the various species.

4.2.9 Coasts of Burma, Thailand, and Malaysia

4.2.9.1 General description. The Indian Ocean coastal areas of Burma, Thailand, and Malaysia are characterized by a long shoreline with many areas of mangrove swamps. These areas are suitable for culture of mussels, prawns, mullets, and other inshore species. The continental shelf, along the coasts of these countries, is 40 to 100 miles wide.

4.2.9.2 Fishing techniques. The fishing gear employed by the Thai and Malaysian fishermen is relatively similar in construction. Fishing is with purse seines of various sizes, traps, and gill nets for the neritic-pelagic species and set bag nets, beach seines, and trawl nets for the semipelagic and bottom species.

4.2.9.3 Species exploited. The data on the unit fisheries of Malaysia (provided by Mr. Soong Min Kong, Director for Fisheries of Malaysia) and Thailand (Tongyai, in press) indicate that the species of fish and crustaceans of economic importance consist of Indian mackerel (Rastrelliger spp.), Decapterus spp., and Stolephorus spp., and wolf herrings for the shelf-pelagic stocks; prawns (Penaeus and Metapenaeus spp.), Lutianus spp., Nemipteridae, and Tachysuridae for the demersal stocks.

4.2.9.4 Present production. Table 3 shows the landings of commercially important species of the west coast of Malaysia for 1965, in decreasing order of importance in terms of economic value.

Table 4 gives the total landings of certain groups of fish on the Indian Ocean side of Thailand.

No production statistics of coastal fisheries of Burma are available.

4.2.9.5 Knowledge of the stocks. Species identification poor. No information on the magnitude of stock sizes in this area. Migrations of the Indian mackerel along the west coast of Malaysia, Thailand, and the coastal waters of Burma are not known.

4.2.9.6 Possible production increase. The production of demersal fishery resources can be increased substantially through the expansion of the trawl fisheries operating on the continental shelf of Malaysia, Thailand, and Burma.

According to Tiews (1966) the trawl fishery on the continental shelf of Burma is capable of producing about 370,000 tons. For Malaysia, Tiews (in press) estimated a production of 600,000 tons.

Improved methods of fishing such as the use of purse seines in combination with light luring techniques, which have been successfully used in the Philippines' basnig fishery, may increase the production of round scad (Decapterus spp.) and Stolephorus spp.

Thailand uses her pelagic and demersal fishery resources in the Gulf of Thailand extensively; however, the resources along the western seaboard of Thailand have not yet been fully exploited. It is expected, however, that the resources in this area will be extensively used by Thailand in the future. During the past two years, the amount of gear fished in this area has increased substantially.

4.2.9.7 Programs of exploration, research, and development. The Department of Fisheries of Malaysia has initiated a program of research on the stocks of Indian mackerels in the area around Penang Island. The biology of the two mackerel species is known fairly

TABLE 3. Estimated landings of commercially important species along the west coast of Malaysia in 1965[1]

Species or group	Estimated annual yield (metric tons)	Value in local currency (Malaysian dollars)
Prawns (Penaeus and Metapenaeus and Macrobrachium spp.)	8,454	7,218,641
Rastrelliger spp.	8,194	6,365,680
Scomberomorus spp.	2,791	5,950,512
Chirocentrus dorab	2,890	5,588,622
Decapterus spp.	5,055	4,276,859
Mollusc (Anadara granosa)	19,381	3,203,730
Lutianus spp.	2,639	3,053,540
Stolephorus spp.	9,172	2,426,048
Clupea spp.	2,625	2,039,988
Mud crab (Scylla serrata)	1,117	1,294,020
Nemipteridae	1,629	1,265,146
Tachysuridae	1,207	937,838
Serranidae	502	913,660
Shrimp (Sergestidae)	3,975	788,580
Carangidae	598	693,840

[1] Statistics obtained from Mr. Soong Min Kong, Director of Fisheries, Ministry of Agriculture and Cooperatives of Malaysia (Ref. (34) in Mal. Fish. 1108).

TABLE 4. Estimated landings of commercially important species along the western seaboard of peninsular Thailand 1964-65[1]

Species or group	Estimated landings in metric tons	
	1964	1965
Rastrelliger spp.	6,331	4,439
Sharks and rays	308	8,685
Miscellaneous fish	13,821	9,162
Shrimps	1,124[2]	740
Cricket lobsters	--	151
Crabs	150	168
Mollusc	233	229
Sea cucumber	2	--
Loligo spp.	--	321
Seaweed	--	16

[1] Statistics obtained from the Statistical Section, Department of Fisheries, Bangkok, Thailand.

[2] Including lobsters.

well. In addition, Malaysia has a trawling survey under way to assess the density of the demersal fishery resources off Penang and Kedah and in Malacca Strait. Also studies on the feasibility of coastal culture of mud crabs and freshwater prawns (*Macrobrachium* spp.) have been started.

Although Thailand has an extensive program to study the stocks of *Rastrelliger* in the Gulf of Thailand, a similar program has not yet been started for the same species in the Indian Ocean. Statistics on the size, maturity stages, and production of the species, however, are presently being compiled. A survey of the density of the stocks of demersal fishes was undertaken in 1964.

4.2.10 West coast of Indonesia. No information is available on the commercially important fisheries of Indonesia. It is expected, however, that the composition of the fishery resources is similar to that in North Australia, Malaysia, Thailand, and Burma. Upwellings are found south of the Sunda Isles.

4.2.10.1 Total production. 85 thousand metric tons in 1958
105 " " " " 1961
110 " " " " 1962
115 " " " " 1963

(Statistics from FAO, 1967.)

4.2.11 West coast of Australia

4.2.11.1 General description. Australia has a long coastline facing the Indian Ocean. The continental shelf is narrow--less than 40 miles--in the southwestern part of the continent. Progressing northward, the shelf becomes wider. In the northwest area of the continent, the prominent shelf exceeds 200 miles in width.

4.2.11.2 Fishing techniques. A list of various fisheries of Australia has been prepared by Kesteven and Williams (1965). Eight commercial fisheries are located along the western coast of Australia (G.L. Kesteven, personal communication). These fisheries and the gear used are:

1. Mandurah estuarine and river prawn fisheries - hand scoop nets
2. Western Australian estuarine and river fisheries - set and haul nets
3. Western Australian salmon (*Arripis trutta*) fishery - beach nets
4. Shark Bay snapper trap fishery - steel-framed, wire-mesh covered traps
5. Western crayfish fishery - crayfish pots
6. Western Australia deep-sea fishery - mesh nets (set) and longline
7. Western Australian deep-sea handline fishery - handline gear
8. West coast prawn fishery - otter trawl nets

4.2.11.3 Species exploited.

Onshore - Mullets (*Mugil* spp., and *Aldrichetta forsteri*), whitings (*Sillago* spp., and *Sillaginodes punctatus*)

Demersal - Crayfish (*Panulirus cygnus* and *Jasus lalandei*), prawns, (*Penaeus* spp. and *Metapenaeus* spp.), sharks and rays, flounders

Shelf-pelagic - *Scomberomorus* spp.

4.2.11.4 Present total production. Table 5 lists the landings of Western Australia and the total Australian landings of five groups of species of commercial importance. It is clear from this table that the most important fishery on the west coast of Australia is the crayfish industry.

4.2.11.5 Knowledge of the stocks. Species identification good for the southern species, poor for the northern species. Australia has carried out biological and population studies on the following species, with the aim of regulating fisheries to obtain optimum sustained harvests:

Australian salmon (*Arripis trutta*)
Western crayfish (*Panulirus cygnus*)
Southern crayfish (*Jasus lalandei*)
King George whiting (*Sillaginodes punctatus*)
Scallop (*Pecten meridionalis*)
Prawns (*Penaeus latisculcatus*, *P. esculentus*, *P. merguiensis*)

4.2.11.6 Possible production increase. Northern coasts of Western Australia are virtually unexplored. A sizable stock of shrimps and prawns may exist in this area.

TABLE 5. Australian marine production, 1964-65[1] (metric tons-estimated live weight)

Group	Western Australia	Australia (total)
Crayfish	7,428	11,898[2]
Perches, croakers, breams, bass, and similar species (including Australian salmon, whiting, and jewfish)	2,898	11,661
Prawns (Penaeus spp. and Metapenaeus spp., etc.)	830	5,476
Mullets, barracudas, and similar species (including sea and yellow mullets)	658	5,779
Sharks and rays	371	4,808

[1] Excerpt from the Production Statistics for 1964-65 of Australia published in Australian Fisheries Newsletter, March 1966.

[2] Total landings of southern, eastern, and western crayfish.

4.2.11.7 Programs for exploration, research, and development. There seems to be no special difficulty in carrying out various programs of research on the aforementioned stocks. It is suspected that the stock of western crayfish is overfished. Australian scientists estimate the optimum yield of crayfish in the west Australian stock to be 7.3 ± 0.9 thousand metric tons. Preliminary regulations of the western crayfish fishery have been initiated by limiting the numbers of fishing boats and the amount of fishing gear, and the introduction of gates in the crayfish pots to allow escapement of small crayfish. The effects of these regulations on the stock are being studied. Preliminary assessments in Shark Bay suggest that the exploitation rate on the prawn stocks is moderately high.

4.3 Inadequacy of statistics from coastal waters

Our attempts to compile information on areas with potential increase of fishery yield have shown that statistics for most countries are inadequate. Lack of division into species groups and of separation of demersal from pelagic-neritic yield, as well as obvious errors in the statistics of a few countries, will hamper attempts to obtain reliable estimates of the fishery resources. We suggest that a first step towards resource evaluation should be an improvement in the statistical recording of fishery data. Data on length frequency, size and sex, and yield per unit of effort for developed and virgin fisheries just being developed should be collected on a regular basis. The collection of these data for the developing fisheries is especially important, since reliable estimates of stock size and natural mortality can be readily obtained at that time, but are extremely difficult to get later.

4.4 Coastal areas and resources of the Indian Ocean requiring attention

From the information compiled above, it is clear that a number of areas or particular stocks show promise of increased yield. These are outlined below.

4.4.1 Bottom trawling on the coasts of Pakistan, west coast of India, Bay of Bengal, and Thailand

Work by Tiews (in press) suggests that a major resource of bottom fishes along these coasts is virtually unexploited. Experimental trawling with trawls adapted for muddy bottoms suggests a potential fishery of between one-half and one million metric tons from this area. These figures are based on shelf regions of the Gulf of Thailand, the Philippines, and the Indian Ocean coast of Thailand (Department of Fisheries, Thailand, unpublished); their extrapolation to the whole shelf area is risky so the above estimate may not be accurate. They nevertheless suggest that a survey of these areas with light trawlers, plus gear of the type proven functional in the Thailand area, is overdue. Yamamoto (in press) showed the varied distribution of trawling effort now put into this area.

4.4.2 The Gulf of Aden and adjacent waters

The productivity figures for the Gulf of Aden suggest an enormous total biomass potential for this area. Both Sardinella and associated small neritic-pelagic species (the seer-fishes) and fish that can be taken by bottom trawl may be present in large numbers. A survey of the productivity (C_{14}) of the area over an annual cycle, combined with a sonar survey of the abundance and distribution of fish schools, over the full area of upwelling, could give vital information to substantiate the estimates based on productivity. The present oceanographic data taken by the Discovery, Anton Bruun, and Vityaz (Kabanova, 1961; Ryther and Menzel, 1965) show so much promise that perhaps too much reliance is being placed on them in the overall view of Indian Ocean potential fish production. The productivity estimates are as yet few in number and do not cover the whole annual cycle. In spite of the lack of close relation between productivity and fishery yield, further productivity and particularly exploration by sonar would be of great aid in obtaining some broad estimate of yield from this area.

4.4.3 Oceanic islands and banks of the western Indian Ocean

The only adequate survey in this area suggested great potential yield of bottom fishes--an estimated 2.8 million metric tons (Wheeler, 1953). Slight expansion of fishing effort is projected for Mauritius. Although the exploitation of such stocks of prime food fishes on rocky bottoms, and far from markets, may be difficult, some reassessment of the potential should be made and consideration of technical improvements in fishing methods should also be made at some stage if this is the vast untapped resource that the Mauritius-Seychelles survey indicates.

4.4.4 Prawn fisheries of the African east coast and Madagascar

In the extensive mangrove areas of Mozambique, Tanzania, Kenya, and Madagascar lies an underutilized prawn resource. Because of the ready sale for local consumption or export, a number of plans to exploit these prawns are under way (Beira Gulf in Mozambique, northwest coast of Madagascar, Rufiji delta of Tanzania). Since problems in these areas may be similar, the rate of development of the prawn fisheries may be accelerated by a rapid exchange of information on techniques of fishing, effect of fishing on stock size and other related problems.

4.4.5 Resources of prawns and bottom fishes of the northwestern coast of Australia

This area is poorly known, but work is projected by the Australian Government in conjunction with industry on prawn resources. It is likely, from recent prawn surveys and industrial ventures in the Gulf of Carpenteria, that the potential for prawn is good. Substantial catches of bottom fishes of good quality were made during a Japanese bottom trawling survey (Masuda et al., 1964).

4.4.6 Estuarine mussel culture

Mussel and fish farming in mangrove estuarine areas may be another means of increasing production. In such areas in the Gulf of Thailand mussels are produced as a by-product of the bamboo stake trap fishery, and landings of *Mytilus maragdinus* in 1961-63 amounted to 70-87 thousand metric tons (Tiews, in press). In the delta area of the Bay of Bengal such an industry may have great potential. These areas cover about 5,000 square miles which gives some indication of the tremendous potential in this type of fish farming (Anon., 1958).

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Blood Types in Fish

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A fascinating exercise designed to acquaint the student with blood typing techniques in humans as well as in fish. This should be a challenge to second-year students.

Introduction

You are all aware that human blood types differ among individuals. Some people are Type O, some are A, some are B and others are AB. These types collectively make up the human ABO blood group system. Blood types in the system are determined by the presence or absence of proteins called *antigens* on the cell membrane of the red blood cells. Blood cells also possess many other antigens; some of them collected in different blood group systems, as for example the Rh system. All these antigens are genetically determined and can be demonstrated by their specific reaction with antibodies contained in blood serum or antiserum.

What is not as commonly known is that the proportions of individuals with different blood types may vary from one human race to another, or from one geographic area to another. For example, if you were to sample the white United States population for ABO blood types you would expect to find about 45% type O, 40% type A, 10% type B, and 5% type AB. If you were to take a racially distinct group and sample in the same way, the percentages could be much different. For example, a sample of Navajo Indians would disclose percentages approximating 70% type O and 30% type A. Thus it is often possible to distinguish human groups on the basis of blood types alone. Such differences in frequencies of blood types can persist only if free interbreeding between groups does not exist. Differences of blood type frequency have been used by anthropologists in the study of human races and in tracing past human migrations.

Demonstration

Within the past 10 years blood typing methods have been applied intensively to the study of fish. It has been found that blood types exist in fish as they do in humans, although the types are not identical. It has also been determined that, as in humans, the frequencies of different blood types vary, depending on the population sampled. This variation is of course an important tool to study intermixing of fish populations, and to trace migrations of geographic groups. This exercise is designed to acquaint you with blood typing techniques in humans and fish, and to demonstrate some of the possibilities for quantitative studies of populations or races by these techniques.

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Materials

Human Anti-A and Anti-B reagents
Hemolets
Alcohol and cotton balls
Microscope slides
Glass-marking pencil
11-x 75-mm culture tubes—100 with rack
1.4% saline
Disposable pipettes and rubber bulbs
5-cc syringes and #20 needles
Centrifuge
Rabbit anti-herring serum (optional)

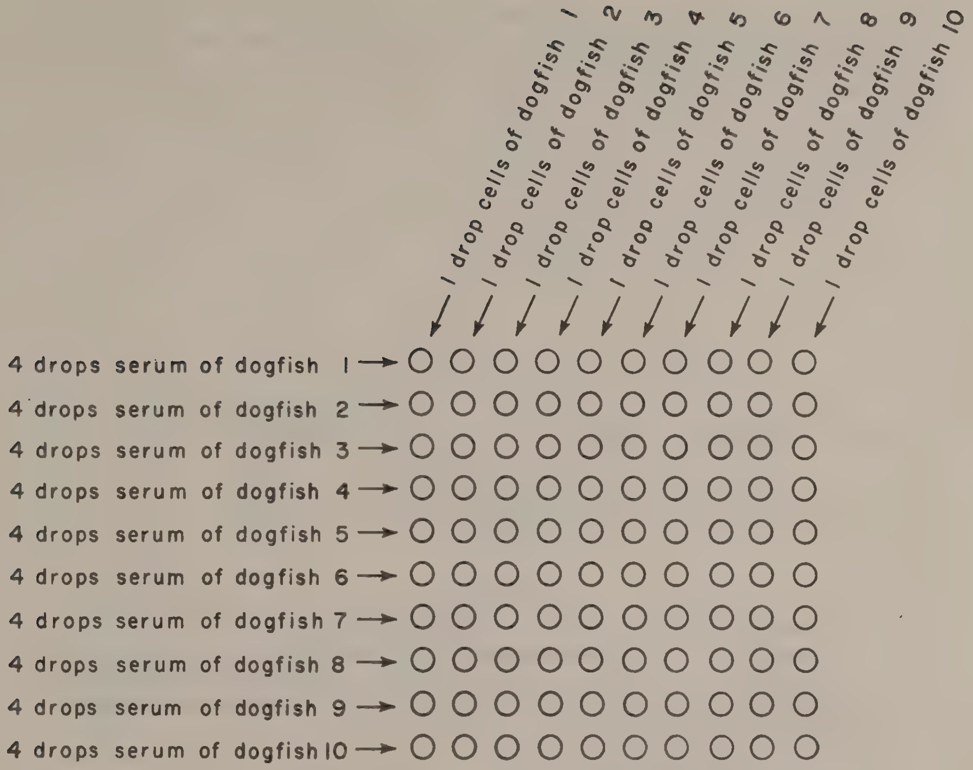
Methods

1. Using Human Anti-A and Anti-B typing reagents from commercial sources, test 10 individuals in class for blood type following instructions on label of reagent bottles. Record frequencies of each type on blackboard and add figures from those not tested who know their blood type. Compare percentages of each type with expected values. (If time is short, it might be possible merely to tabulate types, but it would be preferable to see the nature of agglutination reactions.)
2. Then, demonstrate heart puncture of dogfish and have on hand samples of blood from 10 dogfish bled the previous day. Set up cross-matching of cells of all 10 vs serum of all 10, before class begins, read it at this point and record numbers of S-positives and S-negatives. The S-system of dogfish is actually composed of four blood groups, S_1, S_2, S_1S_2 and S_0. S_1 is detectable with isoagglutinins in serum of individuals that lack S_1 antigen on their erythrocytes; this work is probably as much as can be done in the classroom without prepared antisera. To perform this test, separate serum and cells of 10 fish. Inactivate serum for 1/2 hour at 50°C and dispense four drops horizontally across 10 tubes (11 x 75) mm according to Fig. 1.

   Then prepare 2% suspensions of cells of each fish, washed in 1.5% saline, and dispense one drop vertically through 10 serum tubes, as indicated. This is called cross-matching, and means that cells of all individuals are tested against serum of all individuals. Individuals that possess the antigen lack the antibody, whereas most, but not all, individuals that lack the antigen possess the antibody. A positive reaction is indicated by clumping of cells which may be increased by centrifugation for 30 seconds. Clumps do not break up completely with gentle agitation of the tube. Saline controls should also be used.
3. If dogfish are unavailable, or as an added demonstration, immature herring could be used and tested against rabbit antiserum. This would demonstrate the nature of immunization and specific immune antibodies as an elaboration of the isoantibody system demonstrated in (2) for dogfish but will require advance preparation of antiserum in rabbits. Herring are well suited for this study since they possess an easily demonstrated antigen C, which is dramatically absent in some individuals, and strongly present in most others, yielding a simple C-positive C-negative relationship. Nearly every herring antiserum that we have prepared has been capable of distinguishing C-positive and C-negative individuals.
4. Almost any fish species that is available and large enough to supply a few drops of blood could be used in this exercise, but some preliminary work must be done. Elasmobranchs seem particularly good for demonstration of isoantibody systems. Since few fish species (other than the tunas, salmonids, and clupeoids) have been studied for blood groups, preliminary work might best take the form of cross-matching tests as carried out in step 2. Preparation of rabbit anti-serum can be done, but will require time, animal facilities, and some knowledge of serological techniques.

Expected Results

1. Human blood group frequencies may deviate from expected because of small sample size. This variation could be used as a basis for discussion of sampling of a population.
2. Dogfish (*Squalus acanthias*) in the Gulf of Maine average about 70% S-positive.
3. Immature herring, depending on location, should range from 70 to 98% C-positive.
4. Isoagglutinins and heteroagglutinins oc-


1 drop cells of dogfish 1
1 drop cells of dogfish 2
1 drop cells of dogfish 3
1 drop cells of dogfish 4
1 drop cells of dogfish 5
1 drop cells of dogfish 6
1 drop cells of dogfish 7
1 drop cells of dogfish 8
1 drop cells of dogfish 9
1 drop cells of dogfish 10
4 drops serum of dogfish 1
4 drops serum of dogfish 2
4 drops serum of dogfish 3
4 drops serum of dogfish 4
4 drops serum of dogfish 5
4 drops serum of dogfish 6
4 drops serum of dogfish 7
4 drops serum of dogfish 8
4 drops serum of dogfish 9
4 drops serum of dogfish 10

cur frequently in the elasmobranchs that we have examined, and sporadically in teleost species.

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RECENT ADVANCES IN OYSTER CULTURE IN THE FAR EAST

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(ABSTRACT)

Pressures have been increasing for more effective use of the sea as a food source for an expanding human population, much of which already exists on protein-impoverished diets. Farming the edges of the sea with shellfish as a basic initial crop is an important avenue to increase protein production. Inshore farming is surprisingly advanced in some parts of the world, particularly the Far East where amazing progress in oyster culture has been achieved. The Pacific oyster, *Crassostrea gigas,* cultivated in the Far East, is also grown on the North American west coast—in fact much of the U.S. west coast production is based on seed oysters imported from Japan. Other Asian countries would like to export seed and market oysters to the United States. South Korea and Taiwan have strong economic ties with us, and both are developing oyster culture methods.

South Korean shellfish production is concentrated on the south and west coasts. Particularly in the Pusan area, oyster and mussel culture is well advanced; seed rack systems and rafts are used for off-bottom cultivation. The protected waters on the south coast offer excellent opportunities for expanded production.

Taiwan's oysters are grown principally on the west coast, in the Changhua and Tainan areas. Stick culture, in which bamboo stakes are used, is common, and hanging culture from racks is also used. Taiwan oyster production in 1965 was 18.7 million pounds of shucked meats—a figure not far below Chesapeake Bay's production of 22.7 million pounds.

Two major oyster growing areas in Japan are near Hiroshima on the Inland Sea and near Sendai in northeastern Honshu. Rack-supported seed collectors and bamboo rafts are common culture methods. The recent innovation of long-line culture—float-supported ropes with suspended oysters—is expanding rapidly and permits use of open waters for oyster culture. Japanese oyster production, mostly obtained with off-bottom culture, reached 66 million pounds

in 1965, compared with the total U.S. production of 62 million pounds in that year.

We in the United States have made limited progress toward oyster culture; Long Island has commercial hatcheries and on the west coast Pacific oysters are reared from imported seed from Japan. Many inshore areas along our coasts are amenable to sea farming, and much could be learned from advances being made in the Far East.

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The Effect of the Lamprey Larvicide, 3-trifluoromethyl-4-nitrophenol, on Selected Aquatic Invertebrates

Allen J. Smith

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INTRODUCTION

The chemical compound 3-trifluoromethyl-4-nitrophenol (TFM) is used to control the sea lamprey (*Petromyzon marinus*) in the upper Great Lakes. It is introduced into streams in which sea lampreys have spawned, to kill the larvae. These "treatments" are carried out at intervals shorter than the larval phase of the sea lamprey's life cycle (about

4 to 7 years) to prevent movement of the metamorphosed parasitic lampreys into the lakes.

Most of the streams which contain sea lamprey larvae also have valuable resident fish or serve as spawning and nursery areas for fish of the Great Lakes. These species must be protected from both the direct toxic effects of the control method and from indirect effects such as destruction of food supplies.

Studies by Applegate, Howell, and Smith (1958), Applegate, Howell, Moffett, Johnson, and Smith (1961), and Applegate and King (1962) have all shown that TFM is nontoxic to most species of fish when used at the concentrations that kill larval lampreys. Information on the effect of TFM on aquatic invertebrates is meager. Applegate et al. (1961) reported that TFM was not harmful to selected invertebrates which they included in simulated stream tests. They also stated that no harmful effects to invertebrates were observed during actual stream application. The variety of invertebrate species used in simulated stream tests was limited, and close observation of invertebrates under stream conditions is difficult. Therefore, the present laboratory bioassays were conducted to determine the toxicity of TFM to representatives of a number of groups of invertebrates.

MATERIALS AND METHODS

Tests for most invertebrates were made in 10-liter Pyrex battery jars. Five liters of Lake Huron water were measured into each jar and the jars were placed in a constant temperature trough at 55 F. Test specimens were counted into the jars, and one liter of an aqueous stock solution of TFM of the strength necessary to give the desired test concentration was added to bring the final volume to 6 liters. Dissolved oxygen was maintained with compressed air delivered through a stone air breaker in each jar. Mortality was determined at the end of the test period of 22 to 24 hours. A control jar with 6 liters of water was included with each bioassay.

Some modifications in facilities and techniques were made in the tests of hydras, leeches, snails, and clams. Hydras, because of their small size, were tested in 1-quart Pyrex bowls with approximately 0.6 liter of test solution at room temperature. Leeches, snails, and clams were placed in fresh water for a recovery period of 8 to 10 days after a test because TFM made them sluggish during testing and mortality could not be determined with certainty at the end of the test period.

TABLE 1.—*Test groups and classification of aquatic invertebrates exposed to TFM. (Arranged by phylogeny of Stockard, 1958)*

Phylum and test group	Classification		
	Order	Family	Genus
Coelenterata			
Hydra	Hydroida	Hydridae	*Hydra*
Platyhelminthes			
Turbellarians	Tricladida	–	–
Annelida			
Leeches	Rhynchobdellida	Glossiphoniidae	–
	Arhynchobdellida	Erpobdellidae	–
Arthropoda			
Isopods	Isopoda	Asellidae	*Asellus*
Scuds	Amphipoda	Gammaridae	*Gammarus*
Crayfish	Decapoda	Astacidae	*Cambarus*
Stoneflies	Plecoptera	Perlidae	*Paragnetina*
		Chloroperlidae	*Chloroperla*
		Perlodidae	*Isoperla*
Dragonflies	Odonata	Gomphidae	*Ophiogomphus*
			Gomphus
		Aeshnidae	*Boyeria*
Giant water-bugs	Hemiptera	Belostomatidae	*Lethocerus*
Water boatmen		Corixidae	–
Burrowing mayflies	Ephemeroptera	Ephemeridae	*Hexagenia*
Nonburrowing mayflies		Ephemerellidae	*Ephemerella*
		Heptageniidae	*Stenonema*
		Baetidae	*Isonychia*
Case-building caddisflies	Trichoptera	Leptoceridae	*Triaenodes*
Net-building caddisflies		Hydropsychidae	*Cheumatopsyche*
			Hydropsyche
Blackflies	Diptera	Simuliidae	–
Bloodworms		Tendipedidae	–
Snipe flies		Rhagionidae	*Atherix*
Mollusca			
Snails	Pulmonata	Physidae	*Physa*
Clams	Eulamellibranchia	Unionidae	–

The live specimens were separated into easily distinguishable groups (e.g., dragonflies, damselflies, nonburrowing mayflies) for testing, with the result that some groups included more than one genus. At the conclusion of the bioassay the specimens were preserved and later identified as closely as possible to order, family, and genus (Table 1). Toxicity may have differed among families and genera within test groups but the number of specimens was too small to permit separate calculations. When multiple bioassays were run the data were combined and mortality was computed for the totals.

TABLE 2.— *Percentage mortality of aquatic invertebrates exposed to different concentrations of TFM. (Number of specimens in parentheses)*

Test group	Control	Concentration of TFM in parts per million											
		2	3	4	6	8	10	12	13	14	16	18	20
Hydra[1]	0.0 (25)	80.0 (25)	100.0 (25)	100.0 (25)	100.0 (25)	100.0 (25)	100.0 (25)	100.0 (25)	—	—	—	—	—
Turbellarians	0.0 (5)	20.0 (5)	20.0 (5)	100.0 (5)	80.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)	100.0 (5)
Leeches													
Glossiphoniidae	0.0 (6)	16.7 (6)	0.0 (6)	0.0 (8)	0.0 (7)	0.0 (8)	0.0 (9)	55.6 (9)	55.6 (9)	0.0 (9)	33.3 (9)	0.0 (8)	11.1 (9)
Erpobdellidae	2.9 (35)	3.2 (31)	2.8 (36)	2.7 (37)	23.7 (38)	59.0 (39)	89.2 (37)	100.0 (38)	97.1 (34)	87.9 (33)	97.4 (39)	94.7 (38)	94.6 (37)
Isopods	0.0 (75)	0.0 (75)	0.0 (75)	0.0 (75)	0.0 (75)	0.0 (75)	0.0 (75)	0.0 (75)	1.3 (75)	1.3 (75)	2.7 (75)	5.3 (75)	2.7 (75)
Scuds	4.3 (70)	0.0 (60)	5.8 (52)	0.0 (56)	3.9 (51)	5.9 (51)	0.0 (49)	3.4 (59)	0.0 (48)	5.1 (59)	5.2 (58)	12.5 (48)	10.0 (50)
Crayfish	0.0 (29)	0.0 (29)	0.0 (29)	3.4 (29)	0.0 (29)	3.4 (29)	0.0 (29)	0.0 (29)	0.0 (29)	0.0 (29)	0.0 (29)	0.0 (29)	0.0 (29)
Stoneflies	0.0 (17)	5.3 (19)	0.0 (14)	0.0 (18)	15.4 (13)	15.4 (13)	16.7 (12)	30.0 (20)	31.3 (16)	35.7 (14)	27.8 (18)	33.3 (12)	76.5 (17)
Dragonflies	0.0 (9)	0.0 (8)	0.0 (10)	0.0 (9)	0.0 (9)	0.0 (8)	0.0 (9)	0.0 (9)	0.0 (9)	0.0 (9)	0.0 (10)	0.0 (9)	0.0 (10)
Giant waterbugs	25.0 (4)	0.0 (3)	0.0 (4)	0.0 (4)	0.0 (4)	0.0 (4)	0.0 (4)	0.0 (4)	25.0 (4)	0.0 (4)	0.0 (4)	0.0 (4)	25.0 (4)
Water boatmen	0.0 (127)	0.0 (68)	0.0 (78)	0.0 (71)	0.0 (76)	0.0 (79)	0.0 (91)	0.0 (103)	0.0 (81)	0.0 (87)	2.7 (112)	11.5 (87)	7.8 (102)
Burrowing mayflies[2]	3.0 (33)	10.6 (47)	12.2 (49)	27.7 (47)	62.0 (50)	96.0 (50)	98.6 (1,950)	100.0 (49)	100.0 (49)	100.0 (47)	100.0 (50)	100.0 (48)	100.0 (49)
Non-burrowing mayflies	0.0 (43)	11.1 (27)	0.0 (21)	4.3 (23)	0.0 (23)	0.0 (23)	0.0 (21)	0.0 (24)	0.0 (22)	0.0 (23)	4.3 (23)	32.0 (25)	27.6 (29)
Case-building caddisflies	0.0 (27)	0.0 (26)	0.0 (25)	0.0 (25)	0.0 (24)	0.0 (26)	0.0 (25)	28.0 (25)	0.0 (24)	0.0 (26)	4.0 (25)	0.0 (25)	8.0 (25)
Net-building caddisflies	0.0 (24)	4.2 (24)	8.3 (24)	0.0 (24)	7.7 (26)	20.0 (25)	12.0 (25)	8.0 (25)	15.4 (26)	12.5 (24)	36.0 (25)	26.9 (26)	44.0 (25)
Blackflies	0.0 (15)	26.7 (15)	43.7 (16)	33.3 (15)	66.7 (15)	100.0 (15)	100.0 (15)	100.0 (15)	100.0 (15)	100.0 (15)	100.0 (12)	100.0 (15)	100.0 (15)
Bloodworms	1.0 (101)	1.6 (63)	4.2 (71)	5.0 (101)	6.4 (110)	10.1 (79)	7.1 (98)	5.7 (140)	29.2 (65)	12.0 (83)	17.7 (68)	21.5 (65)	32.3 (65)
Snipe flies	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (5)	0.0 (6)
Snails	6.7 (15)	0.0 (15)	0.0 (15)	0.0 (15)	0.0 (15)	0.0 (15)	0.0 (15)	6.7 (15)	13.3 (15)	6.7 (15)	20.0 (15)	13.3 (15)	13.3 (15)
Clams	0.0 (4)	0.0 (4)	0.0 (4)	0.0 (4)	25.0 (4)	75.0 (4)	50.0 (4)	75.0 (4)	75.0 (4)	75.0 (4)	100.0 (4)	100.0 (4)	100.0 (4)
Sea lamprey[3]	—	57.1 (28)	89.3 (28)	100.0 (28)	100.0 (8)	100.0 (8)	100.0 (8)	100.0 (8)	100.0 (20)	—	—	—	—
Rainbow trout	—	0.0 (24)	0.0 (24)	0.0 (24)	0.0 (4)	0.0 (4)	0.0 (4)	75.0 (4)	60.0 (20)	—	—	—	—

[1] No mortality in an additional bioassay with 25 specimens exposed at 1.0 ppm.
[2] Mortality in additional bioassays was 50.6% at 5.0 ppm (2,043 specimens), and 100% at 15.0 (1,969 specimens).
[3] Additional bioassay run at 1.0 ppm with 20 specimens; no mortality.

The combined data from five bioassays on sea lampreys and rainbow trout (*Salmo gairdneri*) were used to determine the range of concentrations of TFM that would be used for sea lamprey control under the test conditions. These reference bioassays with sea lampreys and rainbow trout were conducted at intervals during the 21-month period when assays were made with invertebrates.

The primary source for invertebrate test specimens was the Ocqueoc River, Presque Isle County, Michigan. A few specimens were collected from other streams tributary to Lake Huron, or from tributaries of Lakes Michigan or Superior. Some specimens were taken from the beach at Hammond Bay on Lake Huron. The insects tested were larvae except for the giant waterbugs and water boatmen, which were adults. Some of the crayfish were young of the year.

Sea lamprey larvae were taken from a laboratory supply collected from streams tributary to Lakes Huron, Michigan, or Superior. The fingerling rainbow trout were supplied by the Michigan Department of Conservation.

TOXICITY TO INVERTEBRATES

Handling and test conditions caused mortalities ranging from 1 to 25% in the controls of 6 of the 20 groups tested (Erpobdellidae, scuds, giant waterbugs, burrowing mayflies, bloodworms, and snails; Table 2). Death did not appear to be entirely dependent on the concentrations of TFM in 11 of the 14 other groups (all except hydras, dragonflies, and snipeflies) which had no mortality in controls but did have some mortality at various concentrations of TFM that may have been caused by handling and test conditions. Interpretation of the tests of scuds was particularly difficult because of irregular kills at the lower concentrations. For both scuds and snails, mortality of control specimens was about half that of animals exposed to 20 ppm, but the constancy of the mortality of concentrations above 13 ppm (scuds) and 10 ppm (snails) indicated slight toxicity to both groups. The effect of TFM on the other invertebrates was more apparent. Concentrations at which mortality approximated 100% were 3 ppm for hydras, 8 ppm for turbellarians and blackflies, 12 ppm for burrowing mayflies, and 16 ppm for clams. None of the other groups suffered a complete kill at 20 ppm. Among the leeches, about 95% of the Erpobdellidae, but only about 11% of the Glossiphoniidae, died at 20 ppm. The mortality of other groups at 20 ppm was about 77% for stoneflies, 44% for net-building caddisflies, 32% for bloodworms, 28% for nonburrowing mayflies, 8% for water boatmen and case-building caddisflies, and 3% for isopods. TFM was apparently nontoxic to leeches of the family Glossiphoniidae (judging by the irregularity of mortality at different concentrations), crayfish, dragonflies, giant waterbugs, and snipeflies.

EFFECT OF TREATMENT CONCENTRATIONS

During application of TFM for sea lamprey control, concentrations are maintained between the minimum lethal concentration (MLC_{100}), which produces 100% mortality of lamprey larvae, and the maximum allowable concentration (MAC_{25}) which does not kill more than 25% of the rainbow trout (Howell and Marquette, 1962). These concentrations are determined by bioassay prior to stream treatment. Bioassays in the field were usually concluded after 20 hours but mortalities that established the limits of the treatment concentration often occurred earlier; actual exposure time during treatment was rarely 20 hours, usually less than 18 hours, and often only 6–8 hours. In the five assays of this study the MLC_{100} was 4 ppm and the MAC_{25} was 10 ppm.

A stream treatment at 10 ppm for a maximum period of exposure would be expected to kill about 100% of the hydras, turbellarians, and blackflies (Table 2). Burrowing mayflies would be reduced about 99%, leeches of the family Erpobdellidae about 89%, and clams about 50%. Mortality among the other groups tested would be less than the 25% allowed for fish. At the lowest treatment concentration of 4 ppm, hydras and turbellarians would suffer kills approximating 100% and burrowing mayflies and blackflies would have kills greater than 25%.

The invertebrates tested, which included members of 5 phyla and 15 orders, represent only a portion of the invertebrates found in sea lamprey producing tributaries of the upper Great Lakes. The variety tested was sufficient to indicate that TFM is potentially toxic to some of the invertebrate fauna. However, TFM at the concentrations used for larvicide treatment does not appear to constitute a hazard to most invertebrates in a stream.

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LAMPREY CONTROL AND RESEARCH IN THE UNITED STATES

by

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U. S. Fish and Wildlife Service

Progress in sea lamprey control was exceptionally good in 1965. Chemical treatment of scheduled Lake Superior streams was completed in October and only the 5 southernmost streams of Lake Michigan remain to be treated. Forty streams discharging 4,127 cfs of water were treated with 74,885 pounds of the lampricide (Table 1).

Table 1. Summary of chemical treatments in United States waters of the Great Lakes in 1965.

	Number of streams	Discharge at mouth (cfs)	Stream miles treated	Lampricide (pounds)	Synergist (pounds)
Superior	16[1]	888	214	12,042	...
Michigan	24[2]	3,239	860	62,843	295
Total	40	4,127	1,074	74,885	295

[1] Includes 15 re-treatments
[2] Includes 9 re-treatments

The number of spawning-run sea lampreys taken at barriers on U.S. streams of Lake Superior remained stable for the third consecutive year, 11,834 in 1965 compared to 11,766 in 1964 and 10,852 in 1963. The Brule River again accounted for more than half (52 percent) of this total. The tagging program has been intensified to attempt to find the source of the lampreys at the barriers.

A most significant advance in knowledge of sea lamprey life history came with the capture of the first adult-phase lampreys from the known-age group in the Garlic River. The minimum age to transformation of the population in this stream is 5 years, and it has been demonstrated that sea lamprey larvae do not all metamorphose on reaching this age.

Lake Superior surveys

Thirty Lake Superior tributaries were surveyed in preparation for chemical treatment or to monitor the re-established populations. Intensive surveys on 5 of these streams, Betsy, Two Hearted, Sucker, Huron, and Brule Rivers, to evaluate magnitude and distribution of sea lampreys, occupied a large part of a field season shortened a month by adverse spring weather. Re-established populations were found in 17 streams, small numbers of residual ammocetes in 10, and no sea lamprey larvae were found in 11 tributaries.

Resurveys of 22 streams considered marginal for sea lamprey production revealed 2 with ammocetes. One ammocete, 87 millimeters in length, was found in the Cranberry River, Bayfield County, Wisconsin, and 8 young-of-the-year larvae were recovered from the Gooseberry River, Lake County, Minnesota. Neither of these streams will contribute significantly to the adult population. Sea lamprey nests were observed in 13 of 25 streams examined for evidence of adult spawning. Minnesota tributaries demonstrated a continued decline of spawning activity with less than 30 nests counted in the 12 streams surveyed. No nests or adults were found in the Split Rock River where 82 and 43 nests were found in 1963 and 1964, respectively. Forty-four nests were counted in 3 areas of the Bad River where 189 nests were located in 1964.

Post-treatment surveys were completed on 20 streams. Small residual populations of lampreys occurred in the Garlic River, Marquette County, Michigan; the Bad River, Ashland County, Wisconsin; and the Sand River, Bayfield County, Wisconsin.

Lake Superior chemical treatments

Chemical treatment of United States tributaries of Lake Superior began in May and continued until the end of October. Generally good treatment conditions existed and problems were few. Sixteen streams with a total discharge of 888 cfs were treated (Table 2). All were re-treatments except the Gratiot River, Keweenaw County, Michigan, which had been reserved as a study stream. Four streams scheduled for treatment during the 1965 field season were not treated. Sullivans Creek, Alger County, Michigan, is a study stream where treatment will be postponed until there is some indication of transformation of ammocetes. Three Mile Creek, Luce County, and Miners River and Five Mile Creek, Alger County, Michigan, contained no sea lamprey larvae. Three Mile and Five Mile Creeks are marginal

Table 2. Details on the application of lampricide to tributaries of Lake Superior in 1965.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm)		TFM (pounds)
			Minimum effective	Maximum allowable	
Anna River	May 18	50	4.0	8.0	594
Mud Lake Inlet	May 26	8	0.5	2.5	54
Little Gratiot River	May 26	100	1.0	3.0	576
Brule River	July 11	210	2.0	4.0	3,510
Two Hearted River	July 30	130	2.5	6.0	2,448
Little Two Hearted River	Aug. 1	32	2.0	5.0	630
Little Garlic River	Aug. 11	5	2.5	7.0	252
Harlow Creek	Aug. 11	10	2.0	5.0	144
Betsy River	Aug. 27	67	2.5	4.0	918
Sucker River	Aug. 29	140	4.0	7.0	1,386
Beaver Lake Outlet	Sept. 8	3	3.0	8.0	144
Furnace Creek	Sept. 22	21	3.0	7.0	144
Garlic River	Sept. 29	18	3.0	5.5	252
Buck Bay Creek[1]	Oct. 6	15	2.0	8.0	180
Huron River	Oct. 20	65	1.0	4.0	702
Gratiot River[2]	Oct. 21	14	3.0	7.0	108
Total	...	888	...	...	12,042

[1] Au Train River tributary treated to keep ammocetes from reaching Au Train Lake.

[2] Initial treatment.

sea lamprey producers at best and the absence of ammocetes was not unexpected. Miners River, however, is not a marginal producer, and the absence of sea lamprey ammocetes may be attributed to the electric barrier near the mouth. These streams will be examined periodically and re-treated when necessary.

The Huron River was not scheduled for treatment until the fall of 1966. However, an intensive survey prompted by the relatively large barrier catch uncovered a small residual and a larger re-established population of larvae. The stream was treated to eliminate the residual population and to estimate the size of the ammocete population present. A known number (3,444) of American brook lampreys was introduced before chemical treatment. These lampreys served as marked individuals since the species does not occur in the Huron River. Collection following treatment of 1,627 sea lamprey ammocetes, 38 newly transformed adult sea lampreys, and 271 American brook lampreys provided the basis for a population estimate of 25,000 sea lamprey ammocetes.

The Brule River, Douglas County, Wisconsin, was re-treated in 1965 to eliminate the recently discovered sea lamprey population above the upstream limits of the 1962 treatment, to check the source of the 88 young adult sea lampreys captured in fyke nets in the fall of 1964, and to see if the population could be the source of the large 1964 and 1965 spawning runs. Surveys made during and after the re-treatment indicated a relatively small ammocete population and it is believed that the large spawning run in the Brule River is due to its location at the west end of Lake Superior in an area lacking other good lamprey spawning streams.

Ammocete collections during chemical treatment continued to demonstrate a decrease in sea lamprey ammocete abundance in most streams. Relatively large re-established populations were found in the lower Brule River, the lower Huron River, and the lower third of the Little Garlic River. A residual ammocete population was discovered in the vicinity of the upper Garlic River's alluvial fan in Sauxhead Lake. An attempt to eliminate this population was made by spraying the area and adjacent waters with chemical during the stream treatment. Four hundred and forty-eight sea lamprey ammocetes were collected within 50 yards of the alluvial fan. No ammocetes were collected beyond this area, indicating that this small ammocete population was localized. This area will be re-treated in the next field season to measure the success of the supplemental treatment.

A fish kill of approximately 14,000 white suckers occurred during the Brule River treatment. No significant fish kills were noted in other streams.

Lake Michigan surveys

Surveys were completed on 17 streams scheduled for treatment along the east shore of Lake Michigan. Intensive effort on the main channels of 2 of the larger rivers, the Kalamazoo, Allegan County, and the Grand, Ottawa County, yielded no larval lampreys. High water temperatures and pollution may be limiting factors in these areas. Lamprey larvae were present in several tributaries to the main streams.

Post-treatment surveys were completed on 20 streams and residual populations of sea lampreys were located in 3. The White River, Muskegon County, produced 3 larvae, while the Ogontz and Whitefish in Delta County produced 15 and 32, respectively.

Lake Michigan chemical treatments

Chemical treatments began in mid-April and ended in late October. Water levels generally were higher than those in the previous 2 years. Twenty-four streams with a total discharge of 3,239 cfs were treated with chemical (Table 3). Fifteen streams received initial treatments. The Whitefish River in Delta County was re-treated after only 2 years because of the presence of numerous residual sea lampreys. Collections during treatment substantiated the presence of ammocetes throughout the watershed and also showed that a strong 1964 year class was present. The many tributaries, springs, beaver dams, and extensive ground water seepage have reduced the effectiveness of treatments in this river. Post-treatment surveys indicate a general, but reduced, distribution of residual sea lampreys after the second treatment.

Surveys of the Grand River, St. Joseph River, and Kalamazoo River main channels failed to demonstrate the presence of sea lampreys. All 6 infested tributaries of the Grand River were treated successfully. Four of the 5 infested tributaries to the St. Joseph River were treated successfully. The remaining tributary will be treated in 1966. In tributaries of both rivers, sea lamprey larvae were absent from the areas of confluence with the main stream. Considering the size of these streams, sea lamprey populations were very small. Apparently lampreys in the Grand and St. Joseph Rivers can be controlled by treatment of the infested tributaries.

Use of the synergistic mixture containing 98 percent by

Table 3. Details on the application of lampricide to tributaries of Lake Michigan in 1965.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm) Minimum effective	Concentration (ppm) Maximum allowable	Lampricide (pounds)
Stoney Creek[1]	April 20	69	5.0	14.0	1,008
White River[1]	May 3	725	4.0	10.0	15,174
Jordan River	May 12	276	5.0	17.0	6,660
Loeb Creek	May 15	6	6.0	17.0	144
Monroe Creek[1]	May 15	10	6.0	17.0	144
Wycamp Creek[1]	May 18	33	4.0	10.0	378
Big Sucker River	May 18	20	4.0	14.0	252
Carp Lake River[1]	May 26	77	2.0	5.0	828
Millicoquins River	May 30	30	3.0	9.0	558
Whitefish River	June 3	363	5.0	13.0	11,034
Little Fishdam River[1]	June 22	15	2.5	8.0	414
Ogontz River	June 24	16	2.0	5.0	207
Big Fishdam River	June 25	50	3.0	8.0	630
Norris Creek[1]	Aug. 11	7	2.0	8.0	90
Grand River[1]	Aug. 19	158	6.0	25.0	4,760
Kalamazoo River[1]	Sept. 10	1,063	4.0	10.0	12,610[2]
Gibson Creek[1]	Sept. 13	2	7.0	20.0	18
Allegan 3 Creek[1]	Sept. 13	1	7.0	20.0	9
Allegan 4 Creek[1]	Sept. 13	1	6.0	18.0	9
Bursaw Creek	Sept. 14	4	7.0	11.0	270
Marblehead Creek	Sept. 14	2	11.0	21.0	90
Brandywine Creek[1]	Sept. 27	10	3.0	10.0	93
Black River[1]	Oct. 6	204	7.0	18.0	4,624
St. Joseph River[1]	Oct. 16	97	11.0	29.0	3,134
Total	...	3,239	...	...	63,138[2]

[1] Initial treatment.

[2] Includes 295 pounds of synergist.

weight of TFM and 2 percent 5,2'-dichloro-4'-nitrosalicylanilide (TFM-2B) was limited to the Kalamazoo River. Although the concentration of TFM-2B was maintained at no more than 2.0 ppm above the minimum concentration of 4.0 ppm, a substantial fish mortality occurred in the main stream. Fish species previously unaffected (gizzard shad, alewife, and longnose gar) were found dead as were large numbers of carp, channel catfish, suckers, and northern pike. Low dissolved oxygen which ranged from 0.6 ppm at the application point to 2.4 ppm at the mouth may have been a factor.

Water quality of southern streams is affecting adversely the biological activity of TFM. Minimum concentrations of 10.0 to 12.0 ppm of TFM are required and little improvement is expected throughout the year. Moreover, most streams south of Muskegon, Michigan are polluted to some degree with industrial wastes which appear to reduce selectivity of TFM. Low dissolved oxygen levels also complicate the situation.

Lake Erie and Ontario surveys

A reconnaissance along the United States shores of Lakes Erie and Ontario in April provided information for planning a more intense stream survey later. Two Lake Ontario tributaries in the vicinity of Watertown, New York, were shocked on the spring trip, and sea lamprey larvae found in the Little Salmon River.

Stream surveys to determine the presence or absence of sea lampreys were initiated on eastern Lake Erie tributaries in September. Four of the 120 streams examined between Conneaut, Ohio, and Buffalo, New York, contained young sea lampreys. Only one stream, Raccoon Creek, produced an appreciable number of individuals, and these were confined to the lower few miles of stream. Conneaut Creek, Crooked Creek, and Cattaragus Creek supported very small populations of ammocetes or transforming adults. Sea lamprey production appears possible in approximately 15 more Lake Erie tributaries in this area, and further work will be required to determine their status. Heavy pollution, small or intermittent stream flows, and other adverse factors render the remaining area streams unsuitable for sea lampreys.

Electric barrier operations

Electric barriers were operated between April 10 and July 13 on 16 streams along the south shore of Lake Superior. A late spring and unseasonably cold weather delayed the installation of the barriers about 2 weeks. A total of 11,834 adult sea lampreys was taken during the period of operation (Table 4). This number is 68 more than in 1964, 982 more than in 1963, but 54,866 less than in 1961 for the same streams. The catch is 77 percent below the 5-year average, 1957-61, before control measures became effective.

The run developed slowly. The first peak (13.6 percent of the total run) appeared between May 26 and 30, and the second peak of 10 days' duration occurred between June 5 and 14 (25.1 percent). The run declined slowly through late June and early July; the last week of operation produced 441 sea lampreys, or 3.7 percent of the run.

The number of sea lampreys from the 11 barriers east of the Keweenaw Peninsula increased 11 percent compared to 1964, while the catch from the western streams decreased 6 percent. The greatest contribution continued to come from the Brule River which produced 52 percent of the barrier catch. However, the run in the Brule River declined 8 percent when compared with the previous year. Increased numbers were taken at 9 barriers. The barriers on the Two Hearted River and the Brule River were the only ones to capture more than 1,000 adults.

Index barriers were operated on 6 streams tributary to Lake Michigan. The 3 barriers on streams tributary to northern Green Bay began operating on April 12-13 and were closed down July 2. The sea lamprey run was delayed by unseasonably cold weather and no lampreys were captured until the first week of May. During the period May 26-30, 27.2 percent of the total catch was taken. The 3 barriers captured 3,277 adult sea lampreys. The catch from these barriers has declined 75 percent since 1961 when 12,886 adults were captured. Two new barriers on the Lincoln and Pentwater Rivers, tributaries to the east shore of Lake Michigan, captured 401 lampreys. The catch from the Pere Marquette River dropped to 311 adult sea lampreys compared to 678 in 1964.

The number of spawning sea lampreys entering the Ocqueoc River, Lake Huron, declined significantly. The Ocqueoc River weir captured 1,390 adults compared to 2,677 in 1964, and 4,674 in 1963.

Data collected from 10 Lake Superior index streams indicate an increase in the size of sexually mature sea lampreys. The average length and weight of the sea lampreys sampled were 16.9 inches and 5.7 ounces as compared to 16.6 inches and 5.4 ounces in 1964. As a group, these are the largest sea lampreys taken at the Lake Superior barriers since 1959. The

Table 4. Catches of adult sea lampreys for comparable periods from 16 Lake Superior streams and 3 Lake Michigan streams, 1960-1965.

Stream	1960	1961	1962	1963	1964	1965
Lake Superior						
Betsy River	696	1,366	316	444	272	187
Two Hearted River	4,290	7,498	1,757	2,447	1,425	1,265
Sucker River	4,683	3,209	474	698	386	529
Miners River	399	220	64	107	74	23
Furnace Creek	2,211	1,012	132	142	93	199
Rock River	2,598	3,660	399	353	229	237
Chocolay River	4,173	4,201	423	358	445	563
Iron River	317	2,430	1,161	110	178	283
Huron River	1,237	4,825	70	201	363	637
Silver River	1,271	5,051	267	760	592	847
Sturgeon River	161	427	397	1,437	375	135
Misery River	696	962	80	24	12	3
Firesteel River	250	1,118	70	178	327	11
Brule River	9,539	22,478	2,026	3,414	6,718	6,163
Middle River	2,815	3,502	311	48	45	52
Amnicon River	1,094	4,741	879	131	232	700
TOTAL	36,430	66,700	8,826	10,852	11,766	11,834
Percentage change		83.1	-86.7	22.9	8.4	0.6
Lake Michigan						
Sturgeon River	910	2,378	1,650	751	823	512
Bark River	1,065	1,085	710	298	202	189
Cedar River	4,676	9,423	5,729	6,412	3,568	2,576
TOTAL	6,651	12,886	8,089	7,461	4,593	3,277
Percentage change		93.7	-37.2	-7.8	-38.4	-28.6

percentage of males entering Lake Superior tributaries continued its downward trend. The 1965 catch contained 52.0 percent males as compared to 54.8 percent in 1964 and 67.1 percent in 1963. This is the lowest percentage of males recorded since 1953.

Adult sea lampreys from the Bark River, a tributary to northern Green Bay, averaged 15.4 inches in length and 4.1 ounces in weight. These are the smallest sea lampreys recorded for this river. Males comprised 58.1 percent of the total number of sea lampreys sampled from the Bark River. This is a significant reduction in the preponderance of males which formed 70.3 percent in 1964.

The average length and weight of sea lampreys from the Pere Marquette River, a tributary to the east shore of Lake Michigan, were 16.3 inches and 5.1 ounces as compared to 15.7 inches and 4.3 ounces in 1964. Males comprised 49.8 percent of the total number of sea lampreys sampled.

Migrant rainbow trout and longnose suckers on 9 representative streams of Lake Superior increased in 1965. A total of 1,319 large rainbow trout was recorded compared to 809 in 1964. The number of white suckers, however, reached a low for the 7-year period.

Sea lamprey wounds were found on 3.2 percent of the rainbow trout entering 9 Lake Superior tributaries. This was a decline of 0.2 percent from 1964, but still 0.5 percent above the number bearing wounds in 1963. At the barrier on the Pere Marquette River (east shore Lake Michigan), 17.0 percent of the rainbow trout captured bore sea lamprey wounds compared with 9.5 percent in 1964.

Movement of tagged sea lampreys in the Great Lakes

The tagging study to provide information on the parasitic phase of the sea lamprey and to determine the degree of interchange among the Great Lakes was continued in the fall of 1965. The tagging operation was expanded to include not only the St. Mary's River, but certain ports on Lakes Superior, Michigan and Huron. The expansion was made possible through the cooperation of the Fisheries Research Board of Canada, the conservation departments of Wisconsin and Minnesota, and many commercial fishermen.

A total of 1,745 sea lampreys was tagged and released between August 19 and December 31, 1965. By December 31, 135 tagged sea lampreys had been recovered, most of them from near the area of release. The following recoveries, however, are significant: 4 adults tagged at Sault Ste. Marie were captured in Lake Superior; 3 tagged near Detour (Lake Huron) were recovered at Sault Ste. Marie; and an adult tagged at St. Ignace was caught off Brevort (Lake Michigan).

The average length of the sea lampreys varied widely in different areas. Lampreys from the St. Marys River at Sault Ste. Marie were the largest. They averaged 17.7 inches (range 11.5 to 25.0 inches) in length, while those taken near Detour were the smallest, with a mean length of 12.8 inches (range 8.9 to 19.7 inches). Sea lampreys from Port Dolomite averaged 13.8 inches, St. Ignace 14.4 inches, and Cheboygan 13.3 inches. For comparison, sea lampreys captured at the Lake Superior barriers in 1965 averaged 16.9 inches in length.

Of the 403 sea lampreys tagged below the navigational locks in the St. Marys River in the fall of 1964, 14 have been recovered. One was taken at the Chocolay River barrier on June 21, 1965, 1 was captured near Gros Cap in Lake Superior, and the other 12 were scattered throughout Lake Huron. Most significant, however, is the recovery of 2 of the tagged individuals in Lake Huron almost a year after tagging. These individuals apparently failed to mature sexually and provide the first indication that the duration of parasitic life in the wild may exceed the commonly accepted period of 12 to 18 months.

Fyke net operations

Fishing of fyke nets in tributary streams to monitor the downstream movements of transforming and larval lampreys was continued in the fall of 1965. Consolidation of weir zones and the increased work load prevented fishing of the nets in the spring. Four newly metamorphosed adults were captured this year in fyke nets which have been fished systematically in 8 Lake Superior streams since 1961. Multiple treatment of these streams has reduced the number of young parasitic-phase sea lampreys taken in fyke nets by 94 percent. Nets fished in Furnace Creek captured 3 transforming sea lampreys and 1 was captured in the Chocolay River.

Nets fished systematically in 5 tributaries of northern Green Bay, Lake Michigan, captured 58 young adults. This is a reduction of over 97 percent from the numbers caught in these streams before chemical treatment. Nets fished in 2 streams (the Sturgeon River net took 44 and the Whitefish River net captured 10) accounted for 93 percent of the total.

Fyke nets were fished in several other streams and locations to assess their effectiveness in providing abundance data and to provide additional information on movement of juvenile sea lampreys within a river system. A total of 13 young adults was captured this year from 3 tributaries of the upper Whitefish River, which enters Green Bay, compared to 146 in 1964. This stream was treated for the second time in 1965. Nets fished in the Brule River (Lake Superior) below a chain of lakes captured 83 individuals in 1964; however, after chemical treatment in 1965, only 2 transforming sea lampreys were caught. Sixty-two newly metamorphosed individuals were captured below Otter Lake in the Sturgeon River (Lake Superior) in 1965, compared to 93 in 1964. Nets fished above Otter Lake took 15 young adults.

Fyke net fishing in 6 streams along the east coast of Lake Michigan was repeated this year. The White River, which received its first chemical treatment in 1965, produced only 1 recently metamorphosed adult compared to 43 individuals in 1964. The remaining 5 rivers were treated prior to the initiation of the fyke net operation. Of these, the North Branch of the Pentwater River produced 6 young adults compared to 2 in 1964; however, the nets were fished for 28 days more than in 1964. In addition, 2 sea lampreys were caught in the Muskegon River.

Recently transformed sea lampreys were again collected from a mechanical screen on the water intake of an industrial plant on the Pere Marquette River. These collections illustrate a drastically reduced production of young adults following treatment of the river with larvicide. Prior to the chemical treatment, 19,793 individuals were taken during the 1963-64 downstream migration. After treatment in May, 1964, only 75 sea lampreys were collected during the downstream migration in 1964-65.

Since the fall of 1962, the Ocqueoc River, Presque Isle County, Michigan, has been fished continuously with fyke nets to study the downstream migrations of sea lampreys. The downstream migration of recently transformed lampreys in the Ocqueoc River starts in October or early November. The migration reaches a peak when stream temperatures drop to between 40° and 44° F in mid-November and continues at a high level until just before freeze-up, in December or early January. The spring migration reaches a peak during the spring breakup. It slackens when water levels begin to drop and is essentially over when water temperature reaches 46° to 48° F. All downstream migration in the Ocqueoc River is over by the middle of May.

The fall migration in 1965 was much larger than in 1964.

In 1964, 960 young adult sea lampreys were captured between the first of November and the last of December in a net which has been fished in the same manner each year. During the same period of 1965, 2,883 individuals were taken in this net.

An attempt has been made to measure the production of transformed lampreys from the Ocqueoc River. A portion of each year's downstream migration was marked with insoluble sulfide dye injection and periodic releases were made above the fyke netting site. A total of 1,320 marked transformers was released in 1963-64, 300 in 1964-65, and 1,200 during the first half of the 1965-66 migration. The ratio of marked to unmarked individuals captured provided a basis for an estimate of production. Extremely high water during the spring peak in 1964-65 prevented a population estimate. The 1963-64 estimate of 42,000 and the 1965-66 estimate of 44,000 for the first half of the run indicate the enormous productive potential of this single river and provide a basis for measuring the effects of chemical treatment.

Re-establishment in treated streams

Seven streams under special study to determine minimum age for transformation have been reduced to 3 by chemical treatments. The treated streams were the Little Garlic and Gratiot Rivers, tributary to Lake Superior, and Marblehead and Bursaw Creeks, tributary to Lake Michigan. All 4 streams contained sea lamprey ammocetes of the 1960 year class but transforming sea lampreys were recovered in 1965 from only 3. Although the growth rate of the Gratiot River ammocetes appears to approximate the growth in the other 3 streams, no transformation was evident. These observations suggest that in most Lake Superior tributaries sea lampreys begin to metamorphose in 5 years. Ammocetes in the 7 study streams, however, have not shown the rapid rate of growth found in some of the large Lake Superior tributaries such as the Bad, Sturgeon, and Ontonagon Rivers. Frequent re-treatments were necessary in these streams to eliminate residual populations. Consequently, information necessary to indicate the minimum time to transformation could not be obtained. The possibility of metamorphosis occurring in less than 5 years in streams where ammocetes demonstrate rapid growth should not be overlooked.

The 3 remaining study streams containing ammocetes of the 1960 year class are Snyder-Deadhorse and Hog Island Creeks, tributary to Lake Michigan, and Sullivans Creek, tributary to Lake Superior. Growth rates of sea lamprey larvae in these streams are significantly slower than in the 4 treated streams. During 1965, very few larvae more than 120 millimeters in length were recovered from each creek, and there was no evidence of transformation. Continued monitoring of these streams should provide information on the potential of small streams to produce adult sea lampreys.

The reduction in the number of streams with re-established populations and the relative abundance of sea lamprey ammocetes has paralleled the decline of adults taken in the electric barriers. The collection of young-of-the-year larvae this year was hampered by bad weather and unfavorable stream conditions, but it appears that low recruitment will continue. In Lake Superior tributaries, the 1960 and 1961 year classes are now found only in Sullivans Creek. The 1962 year class is found in 6 streams including Sullivans Creek. The 1963 and 1964 year classes are found in 12 and 17 streams, respectively. The 1965 year class has been found in 13 streams in a preliminary survey.

Lake-dwelling ammocete populations

Concern as to the significance of lake-dwelling larvae prompted further work in Lake Superior. Tows with an electric trawl totaling 28 hours were made at 15 locations and sea lamprey ammocetes captured in Furnace Bay, Huron Bay, and off the mouths of the Little Garlic and Brule Rivers.

The trawl captured 7 sea lamprey and 34 native ammocetes in Furnace Bay. The rate of capture for sea lampreys was only 2.2 individuals per 100 minutes of towing time compared to 13.0 in 1964, 17.2 in 1963, and 15.4 in 1962. Eight larvae were taken off the mouth of the Little Garlic River during 209 minutes of towing time. The shallow inshore waters off the mouth of the Brule River produced 8 sea lamprey and 2 native ammocetes in 145 minutes. A series of tows in water 80 to 110 feet deep, however, was unproductive. Tows cannot be used effectively below 110 feet. The deepwater tows produced a large number of *Mysis relicta*. Only 1 sea lamprey ammocete and 49 native ammocetes were captured in Huron Bay in 95 minutes of towing time. The relatively small population of sea lampreys in Huron Bay as indicated by the electric trawl was verified by an extensive search for ammocetes in shallow waters with shocking equipment. Several hours of collecting produced 238 native and 3 sea lamprey ammocetes.

Further trawling was done in Otter Lake in an effort to locate the source of newly metamorphosed adults taken in the fall of 1964 by fyke nets in the Sturgeon River below the lake. The trawl took only 4 native ammocetes in 197 minutes of towing time. Hand shocking for 3 hours in shallow water using power from electrical equipment on the trawl boat produced 1 sea lamprey and 16 native ammocetes. The sea lamprey was taken in the Sturgeon River at the outlet of the lake.

Trawling in Lake Michigan waters was limited to 2 areas. Trawling for 110 minutes near the mouth of the Ford River resulted in the capture of 1 sea lamprey ammocete. Extensive trawling in the lower 15 miles of the Grand River was negative.

Sea Lamprey research

The dominant research activity continues to be the development of less costly and more effective larvicides. Studies of the factors which have limited the usefulness of the synergistic mixture TFM-2B in tributaries of Lakes Michigan and Huron, and clearer definition of the toxicity of this compound have received major emphasis. A limited amount of work on salicylanilides, other than Bayer 73, also has been continued. "Rough screening" of new compounds has been curtailed.

Development of larvicides. Fish kills with TFM-2B in the relatively hard-water streams tributary to Lake Michigan prompted a study designed to elaborate, as completely as possible, the toxicity of the mixture and its component chemicals in waters from streams of all the upper Great Lakes. Bioassays were run with TFM, TFM-2B, and Bayer 73 in waters from 13 sources. Assays with these materials were conducted simultaneously in a single sample of water from each source to permit direct comparison of results. Increasing water hardness (calcium carbonate content), which is known to reduce the biological activity of TFM was shown to have a similar effect on TFM-2B and Bayer 73. In addition, each water sample was analyzed for conductivity, pH, calcium, chlorides, copper, ferric iron, ferrous iron, ammonia nitrogen, nitrate, nitrite, sulfate, silica, tannin and lignin, ortho phosphate, meta phosphate, and dissolved carbon dioxide. None of these measurements correlated better with toxicity than water hardness.

The toxicity data obtained for larval lampreys and rainbow trout with TFM-2B, TFM, and Bayer 73 in each of the 13 test waters again indicated a considerable amount of synergism when Bayer 73 and TFM compounds were mixed. Only in very soft or hard waters did the concentration of either compound alone produce significant lamprey mortality. In 7 of the 13 water sources the expected rainbow trout mortality with Bayer 73 was greater than observed with the mixture. In these waters, it would appear that mixing with TFM reduced the toxicity of Bayer 73 to rainbow trout. In the remaining 6 waters, the combined expected mortality for the 2 chemicals used separately was less than the mortality observed with the mixture. Mixing the 2 compounds, therefore, had a synergistic effect on their toxicity to rainbow trout. The different behavior of the mixture could not be related to the chemical and physical conditions.

Additional bioassays were conducted with TFM and Bayer 73 to investigate more thoroughly their relative toxicity. These assays were with Lake Huron water and mixtures containing from 1 to 10 percent Bayer 73. Each of the mixtures indicated a high level of synergism in toxicity toward larval lampreys. The level was greatest at 2 and 3 percent since the combined expected mortality figures were the lowest with these mixtures. The depressant effect of TFM on the toxicity of Bayer 73 to rainbow trout was pronounced in mixtures from 2 to 10 percent. In all except the 1 to 10 percent mixtures the amount of Bayer 73 was sufficient to produce over 90 percent mortality even though the mixtures themselves killed only 25 percent of the rainbow trout. Why the toxic effect of Bayer 73 should be less when it is mixed with TFM is difficult to explain without detailed knowledge of the physiological action of the compounds.

Although the toxicity values themselves did not indicate the reason the TFM-2B mixture should be difficult to use under field conditions, the series of regression lines which were derived with various mixtures provide some insight to the problem. These lines are extremely steep (slope functions 1.2 ± 0.1) and parallel. Therefore, small fluctuations in the percentage composition of the mixture drastically affect the toxicity. As an example, the data obtained in Lake Huron water indicate that 6.95 ppm of TFM-2B (2.0 percent Bayer 73) will produce a mortality of 25 percent among rainbow trout. If a mixture containing 2.5 percent Bayer 73 was applied at the 6.95 ppm level, the expected mortality among trout would be 70 percent. Fluctuations of 0.5 percent or more in the Bayer 73 component are difficult to prevent with present methods of application.

Screening of new chemical compounds. Screening of previously untested compounds has been reduced during the past year. A total of 126 chemicals was tested for the first time in 1965. Sixty-one were nontoxic to larval lampreys at the initial screening level of 10.0 ppm. Among the compounds toxic to larval lampreys, 37 were active at concentrations from 10.0 to 1.0 ppm, 26 from 1.0 to 0.1 ppm, and 2 from 0.1 to 0.01 ppm. Twenty-six chemicals indicated some degree of selective toxicity toward larval lampreys.

Larval growth and transformation. For a number of years, experiments have been underway to evaluate the effect of supplemental feeding on ammocetes held in aquaria. Results from these experiments consistently have indicated poor survival, growth, and almost no transformation among larvae held in only Lake Huron water. In those groups receiving supplemental feeding, survival, growth, and transformation have been near that expected in the better lamprey-producing streams. While the results obtained can not be considered as conclusive, they do indicate that the food resources available to larvae in Lake Huron may not be sufficient to permit survival.

Experimental population of ammocetes. The experimental population of known-age ammocetes established in the Garlic River in 1960 produced its first adult-phase sea lampreys. During the year, 4 young adults were captured at the downstream trap. Two had been captured as ammocetes, marked, and released in the study area.

A total of 733 ammocetes was collected and examined during October for annual growth information. None of the ammocetes showed signs of metamorphosis. The capture of 4 recently metamorphosed juveniles and data provided by the October collection established the minimum duration of larval life for this population at 5 years, and proved that metamorphosis for all individuals in a single age group did not occur at the same age, but would continue over a period of years. The rate of growth for the past year and the range in lengths for the ammocetes were comparable to 1963 and 1964 (Table 5). The ammocetes had a mean length of 107 millimeters and ranged from 65 to 176 millimeters. The recently transformed adults

Table 5. Growth of 1960 year class of ammocetes in the Garlic River to October, 1965.

Year	Mean length	Length range	Length increment
1960	13 mm	10- 19 mm	13 mm
1961	39 mm	25- 54 mm	26 mm
1962	63 mm	37-107 mm	24 mm
1963	80 mm	52-134 mm	17 mm
1964	94 mm	43-159 mm	14 mm
1965	107 mm	65-176 mm	13 mm

were 152, 155, 161, and 172 millimeters long. Only 2 percent of the ammocetes in the October 1964 collection were as large or larger.

The downstream trap captured 4,340 lampreys in 1965 compared to 2,847 in 1964, 370 in 1963, and 9 in 1962. The period of major downstream drift for ammocetes was from April through June.

Since October 1962, 5,642 ammocetes have been marked and returned to the study area. Only 16 marked individuals, including the 2 recently metamorphosed adults, were taken at the trap during the year. The annual October collection made with an electric shocker, however, contained 143 marked individuals. Three were marked in 1962, 4 in 1963, 31 in 1964, and 106 were from the 1965 group. One ammocete had been marked twice.

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MULTIPLE MOLECULAR FORMS OF SERUM ESTERASE IN THREE TUNA SPECIES FROM THE PACIFIC OCEAN

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MULTIPLE MOLECULAR FORMS OF SERUM ESTERASE IN THREE TUNA SPECIES FROM THE PACIFIC OCEAN

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INTRODUCTION

THE discovery of the technique of starch gel electrophoresis by Smithies (1955, 1959) and the discovery by Hunter and Markert (1957) that enzymes migrating in the starch gel could be made directly visible by histochemical staining techniques have led to the recognition and description of multiple forms of numerous enzymes in plants and animals. Hunter and Markert (1957) termed the starch gel with its visible enzymes, a zymogram. Shaw (1965) and Beckman (1966) have reviewed the pertinent findings to date in animals and man. Frequently when multiple molecular forms of enzymes have been described, specific modes of inheritance have been proposed to account for the molecular variations (Shaw, 1965; Beckman, 1966).

In *Peromyscus*, the deer mouse, Randerson (1964) has proposed a system of three alleles, "C, D, e", to account for the observed polymorphisms in tissue esterases. Gahne (1965) described variation of plasma esterase in the horse and, on the basis of sire family data, accounted for the six observed phenotypes as the products of a series of four multiple alleles. In both of the above studies, the authors presented evidence for the segregation of one recessive allele which in homozygous condition leads to the total absence of esterase activity.

Nyman (1965) reported variation of serum esterase in the fresh-water roach (*Leuciscus rutilus*). Three esterase phenotypes were observed in a sample of 300 individuals; the proportions of individuals in the three phenotypes were in close agreement with that expected from a Hardy-

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Weinberg equilibrium. No photographs or details as to buffer system, or staining procedures were given in NYMAN's report.

Attempts to develop genetic marker systems in fishes for use in studies of population heterogeneity are becoming increasingly widespread, as discussed by MARR and SPRAGUE (1962), and reviewed by CUSHING (1964). The majority of marker systems identified in fishes between 1952 and the present, have been those inferred from studies of erythrocyte antigens. Recently, however, a rapid development of additional genetic markers in various species of fish is indicated by studies of hemoglobins of cod by SICK (1966, a, b), of lactate dehydrogenase in a variety of species of fish by MARKERT and FAULHABER (1965), of lactate dehydrogenase and aspartate aminotransferase in the Atlantic herring (*Clupea harengus harengus* L.) by ODENSE *et al.* (1966) and of serum protein variation in the skipjack tuna (*Katsuwonus pelamis* L.) by SPRAGUE and FUJINO (1965).

This report describes multiple molecular forms of serum esterase in three species of tuna, and, on the basis of population data, a genetic hypothesis is proposed to account for the esterase variants. The species are the bigeye tuna, *Thunnus obesus* (LOWE), the southern bluefin tuna, *Thunnus maccoyii*, and the yellowfin tuna, *Thunnus albacares* (BONNATERRE).

Materials and methods

The material for this study was obtained by bleeding tunas from the heart with a needle and syringe. The tunas were always bled within a few minutes to a few hours after capture. The sera have been stored at −10° C since collection.

The sera of southern bluefin tuna were obtained by the CSIRO of the Australian government between April 1964 and June 1965; sera from 107 bigeye tuna were collected in July 1966 by the U.S. Bureau of Commercial Fisheries Research Vessel CHARLES H. GILBERT; and 79 bigeye tuna and 46 yellowfin tuna were collected at the fresh-fish market, Honolulu, Hawaii, by Bureau of Commercial Fisheries personnel in August and September 1966.

The sera were subjected to starch gel electrophoresis in acetate buffer, pH 5.5, for 4 hours at 30 V/cm and in a discontinuous buffer (ASHTON and BRADEN 1961), pH 8.5, for 2 hours at 30 V/cm. For the visualization of esterase activity, alpha-napthyl acetate was used as a substrate and fast red TR salt as a coupling agent. Betanapthyl acetate

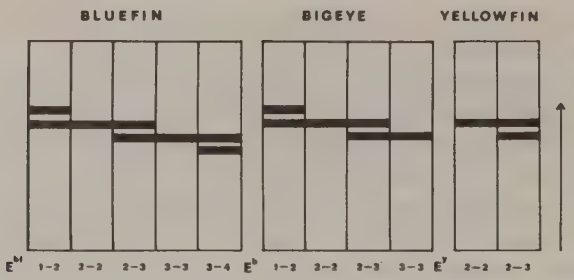

Fig. 1. Schematic representation of the serum esterase types of southern bluefin tuna, bigeye tuna, and yellowfin tuna. The arrow indicates the direction of mobility towards the anode.

and fast garnet GBC salt are also useful as a substrate and a coupling agent in this material.

The presence of sialic acid on the esterase molecules was examined by incubation of sera with equal amounts of neuraminidase solution (Behringwerke) for 4 hours at 37° C.

RESULTS AND DISCUSSION

Zymograms of erythrocyte-free tuna serum exhibit one distinct zone of esterase activity. Electrophoretic variations were seen at pH 8.5 and pH 5.5 but unequivocal classification of the phenotypes recognized at pH 5.5 is not possible at pH 8.5. Zymograms of sera containing large amounts of hemolyzed red blood cells exhibit additional zones of esterase activity. These erythrocyte esterases will be reported on elsewhere.

The observed phenotypes of individuals of the species—southern bluefin tuna, bigeye tuna, and yellowfin tuna—are shown schematically in Figure 1. As many as four different electrophoretic variants were found in the bluefin tuna (see also Fig. 2). In the bigeye and yellowfin tunas the numbers of electrophoretic variants were three and two respectively.

Table 1 shows the results of testing sera of 70 southern bluefin tuna. The relative proportions of individuals in the five phenotypes are in close agreement with the Hardy-Weinberg expectation assuming the existence of four alleles in the frequencies $E_1^{bf}=0.0073$, $E_2^{bf}=0.809$, $E_3^{bf}=0.176$, $E_4^{bf}=0.0073$.

Two of the 70 southern bluefin tuna reported in Table 1 showed no

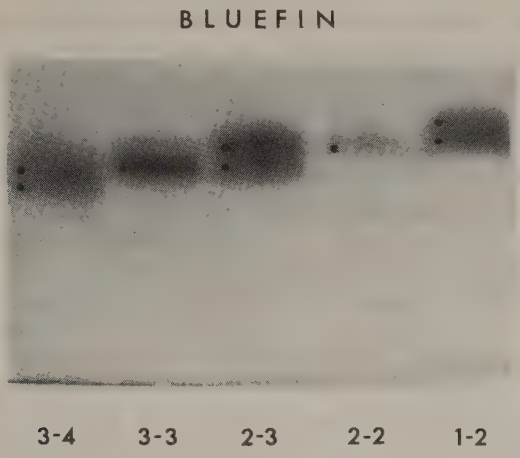

Fig. 2. Photograph of starch gel zymogram showing the five different esterase types observed in southern bluefin tuna.

esterase activity. It may sometimes be difficult to distinguish between a genetically determined enzyme deficiency and the uncontrolled deterioration of the esterase activity due to the length of storage of the samples. For example, sera of 30 southern bluefin tuna, all stored for more than 2 1/2 years, have not been included in the data because the esterase activity was very weak.

Table 2 summarizes the results of testing 184 samples of bigeye tuna for esterase type. At least three alleles are proposed to account for the observations in Table 2. The Hardy-Weinberg expectations assuming three alleles with frequencies $E_1^b=0.0055$, $E_2^b=0.9171$, $E_3^b=0.0773$ are in close agreement with the observations reported in Table 2. The ob-

TABLE 1. *Observed and expected numbers of bluefin tuna in the esterase types $E^{bf}1$—2 through $E^{bf}3$—4.*

Of the 70 fish tested, 2 were esterase-negative $E^{bf}O$.

	Southern bluefin tuna esterase types (E^{bf})				
	1—2	2—2	2—3	3—3	3—4
Observed	1	47	15	4	1
Expected	0.8	44.5	19.4	2.1	0.2

TABLE 2. *Observed and expected numbers of bigeye tuna in the esterase types E^b1—2 through E^b3—3.*

Of the 184 fish tested, 3 were esterase-negative E^bO.

	Bigeye tuna esterase types (E^b)			
	1—2	2—2	2—3	3—3
Observed	2	152	26	1
Expected	1.8	152.2	25.7	1.0

servation of three esterase-negative bigeye tuna cannot be accounted for by means of sample age, or the age or sex of the fish. It is possible but not probable that the samples were inadvertently inactivated in collection. In view of the previously cited examples of recessive alleles in the esterase systems of *Peromyscus* and the horse, it is likely that more detailed studies of the esterases of bigeye tuna will provide evidence for the existence of a recessive allele in that species and possibly other tuna species as well.

The enzyme activity showed considerable variation. It was possible to classify the samples into two groups with strong and weak esterase activity. Table 3 shows the results of classifying 69 adult bigeye tuna for sex, electrophoretic variations, and esterase activity. The sex difference was significant ($0.05 > P > 0.01$); females were more often of the "strong" esterase type. Since the serum samples from all individuals

TABLE 3. *Classification of 69 bigeye tuna according to sex, electrophoretic variations, and esterase activity.*

Phenotype	Esterase activity			
	"Strong"		"Weak"	
	Male	Female	Male	Female
E^b 1—2		1		
E^b 2—2	5	11	23	18
E^b 2—3		4	3	3
E^b 3—3		1		
Total	5	17	26	21

were collected at the same time and have been treated in the same way, it is unlikely that the variations of strength are storage artifacts. No definite conclusions can be drawn concerning the cause of the strength variations but among the possible interpretations is control by sex-linked genes. No information was available as to the sex of 115 immature bigeye tuna among the 184 tested. Similar tabulations were made for 58 adult southern bluefin tuna and 46 adult yellowfin tuna. Sex and esterase activity were not correlated.

In tests of 46 yellowfin tuna, 44 (.957) were of phenotype E^y2—2, and 2 (.043) were of phenotype E^y2—3. Two alleles (E_2^y, E_3^y) are postulated to account for these observations.

Incubation of the unstained gel with 10^{-2} molar EDTA and 10^{-4} molar eserine for 30 minutes at 37° C did not inhibit the subsequent esterase staining of the gel. On the basis of these observations, the major serum component of tuna appears to be an aliesterase or B-esterase (AUGUSTINSSON, 1961). Treatment before electrophoresis with neuraminidase causes retardation of the treated sample as compared with the control; thus the esterase molecules carry sialic acid.

As can be seen schematically from Figure 1, the electrophoretic mobilities of the serum components of tuna esterase are very similar. Similarities also exist in the type of polymorphism observed; the nomenclature presented is not intended, however, to suggest either chemical or genetic homology between the different esterase variants of the tuna species investigated. The nomenclature is flexible, providing for the numbering of new types in the order of discovery.

Acknowledgements. — I wish to express my appreciation to Dr. LARS BECKMAN for his encouragement, interest, and valuable suggestions in this study.

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SUMMARY

The electrophoretic variations of serum esterase were studied in three species of Pacific tunas. Polymorphic esterase phenotypes were observed in each of the three species. Five phenotypes were seen in southern bluefin tuna, four in bigeye tuna, and two in yellowfin tuna. On the basis of population data, a series of multiple alleles in each species has been proposed to account for the serum esterase phenotypes observed.

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SHARK RESEARCH

by Stewart Springer, Shark Research Panel, American Institute of Biological Sciences

THE PUBLICATION IN 1948 of the volume on sharks in "Fishes of the Western North Atlantic" marked the beginning of a renewed interest throughout the world in the biology of sharks.

The need for more information about these important animals had become clearly apparent in the United States during World War II, when 90% of the vitamin A used in the rapidly developing poultry industry was obtained from shark-liver oil. Also, the extensive marine and amphibious military operations during the war drew attention to sharks as a hazard to man.

Production of shark-liver oil in the U.S. practically ceased in 1950 due to the development of a cheaper, partially synthetic source of vitamin A. And although the need to cope with the shark hazard no longer appeared so acute to the armed forces, new pressures to learn more about sharks developed.

The realization that it is urgent for man to make the best use of renewable food resources of the sea has again focused attention on sharks and their relatives, not only as competitors of man in the harvest of seafoods but also as an under-utilized food resource.

The increasing use of the sea by man for recreation, mining, and for paramilitary operations makes it more important than ever for man to understand the shark hazard.

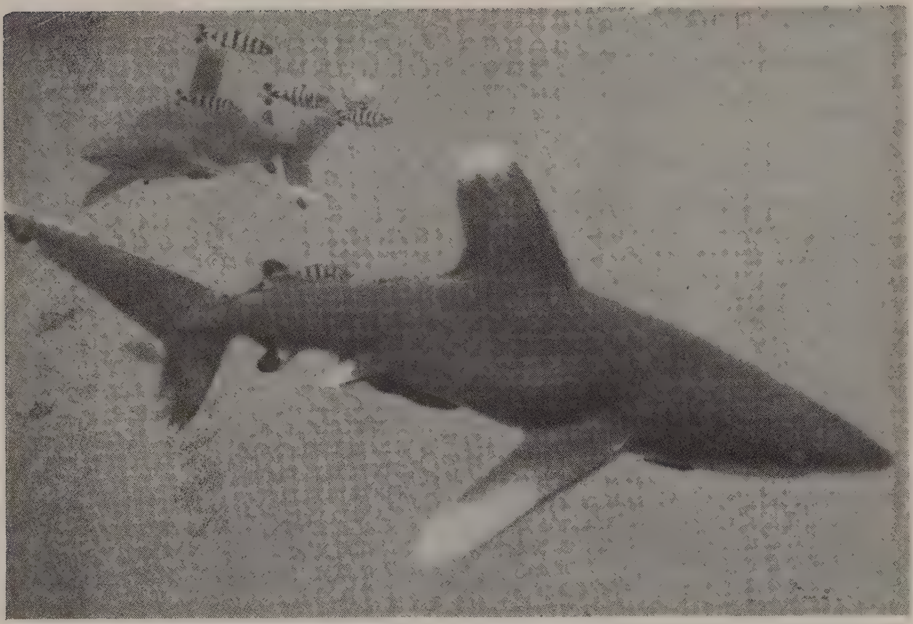
Finally, a substantial increase in basic biological research on the cartilaginous fishes, including sharks, has developed from interest in these vertebrates as representative of a group that has met the challenges of changing environments over the ages in somewhat different ways than other vertebrates. Physiological, behavioral, and ecological studies and experiments with sharks sometimes furnish new insights and approaches to persistent problems of man.

The response of the scientific community to the need for a better and more comprehensive understanding of sharks has lagged somewhat but is now growing substantially. In the U.S., the Office of Naval Research led the way in its support of basic investigations of shark biology.

The Bureau of Commercial Fisheries also has supported basic research on sharks in its role as a proponent for the optimum management and utilization of food resources from the sea. The American Institute of Biological Sciences, through its Shark Research Panel, has contributed a substantial input in the stimulation and coordination of studies of sharks.

The diversity of recent interest and institutional affiliation of research workers can be seen in two volumes, "Sharks and Survival," with 20 authors, published by D. C. Heath in 1963, and "Sharks, Skates, and Rays," with more than 40 authors, scheduled for publication by the Johns Hopkins Press in 1967.

The difficulties attending attempts to make significant progress with the applications of science, on the basis of fundamental knowledge that is 20 to 50 years behind the times, are nowhere more clearly indicated than in current questions about the importance of sharks as a resource and as a hazard. Progress toward an understanding of sharks and their role now is being made, but much remains to be done. ☐



WHITE TIP SHARKS *with a retinue of pilot fish were photographed from the raft* Nenue *during a Bureau of Commercial Fisheries study of the behavior of Pacific pelagic fishes.*

Reprinted from Sharks, Skates, and Rays. The Johns
Hopkins Press, Baltimore, Md., 1967

9

SOCIAL ORGANIZATION OF SHARK POPULATIONS

Stewart Springer

The purpose of this paper is to assemble observations on the behavior and distribution of sharks and to make deductions on the nature of the social organization of shark populations. The subject must be treated in a cursory way because little is known of the group behavior of sharks or even of the salient features of the life histories of most of the 250 or more species. Nevertheless, many aspects of the biology of sharks are more easily understood when the varied strands of evidence about their social behavior and the structure of their social organizations are brought together.

Many of the observations reported here are my own and were made while I was engaged in field work in the shark fishery (1) as a commercial collector of biological specimens and part-time as a shark fisherman, chiefly in the Gulf of Mexico, 1930–40; (2) as a fisherman and production supervisor, with assignments in exploratory fishing and in research on the shark hazard to man, 1940–50 (a substantial amount of time during this period was spent on commercial shark-fishing vessels operating from the Virginia Capes to the mouth of the Amazon River); and (3) as a biologist during many cruises of the R/V *Oregon*, a Bureau of Commercial Fisheries exploratory fishing vessel, in the Gulf of Mexico and northern Caribbean Sea, 1950–55.

Before undertaking an account of shark societies, I wish to review briefly some aspects of the evolutionary history of sharks and to mention some of their specializations for the prenatal nourishment of comparatively large young. The position of sharks as predators and as prey also is worth some preliminary comment because the aggressive, predatory habits of some species would severely limit distribution and threaten the survival of species if they were not prevented from predation by a social organization. Since much of the evidence of shark social organization is derived from observations of distribution of several elements of each population, some general comments on shark distribution seem in order, and I have included here also a representative distribution of a migratory shark population that frequents shore waters.

Common names that are used wherever possible throughout the paper follow the American Fisheries Society (1960) list. Equivalent scientific names for species mentioned are given on pages 171–172.

NATURAL HISTORY OF SHARKS

Evolutionary Stability

The evolutionary line of descent of sharks was distinct from other lines leading to modern vertebrates in the late Devonian period, some 400 million years ago. Except for some periods of speciation and adaptative radiation, with one important branch leading to the skates and rays, the sharks have remained remarkably stable. Among those living at the present time, members of one small family of about 20 species, the horn sharks or Heterodontidae, bear some resemblance to certain Paleozoic hybodonts. These may represent one line of descent that has always inhabited inshore waters. The horn sharks are not now abundant and are restricted to habitats of a small area. All other modern sharks appear to be derived from deep-water stocks, and the present-day sharks that are structurally more generalized live for the most part in relatively deep and cool waters.

J. Z. Young (1962) stated the following.

> It is not clear that the group [the elasmobranchs] has advanced, in any sense, since the Devonian. The type has always been a successful one, able to produce specialized carnivores. We do not know enough to be sure whether the number of creatures with this organization has changed greatly, but it seems that, except for a reduction in numbers in the Triassic, they have always been abundant and are perhaps at present on the increase.

Although Young's view may be a simplified one, it is basically tenable and raises the question of why sharks were able to persist through the ages despite changes in environment and increases of fitness of competing organisms. Our knowledge of the history of shark evolution is of course derived from the fossil record, which shows principally the gross anatomical features of sharks in chronologically successive faunas. Fossils reveal little of the ecology of extinct forms and nothing of the physiology beyond what can be deduced from structural features of the animal or from estimates of the environment. Perhaps sharks have persisted because they were able to make physiological and behavioral changes without accompanying changes in gross morphology.

The Development of Large Young

Sharks tend to produce small numbers of large young. Fertilization is internal in all modern sharks, and the presence of claspers in the better-known Paleozoic hybodont sharks indicates early appearance of internal fertilization. Among living sharks, the Heterodontidae and Rhincodontidae and most species of the Scyliorhinidae and Orectolobidae produce large eggs laid in leathery egg cases. All other sharks about which information is available give birth to young capable of swimming away on release from the oviducts of the mother as smaller copies of their parents. The number of young sharks produced or the number of eggs laid in a season is relatively small. In many species, less than a dozen are produced and, as far as is known, never more than 114. The gross morphology of the reproductive organs of elasmobranchs departs comparatively little from a general pattern except that in the more specialized sharks only one ovary is functional and in some of the rays only one oviduct is functional.

A great variety of specializations provides for the nourishment of shark embryos to bring them to large size: the production of few eggs with very large yolks; the utilization of more than one yolk by a single embryo; the ingestion of egg yolks and other embryos by sharks emerging from egg cases that have been held in the oviducts of the mother; and the presence of a means for the transfer of nutrients from the mother to the developing embryo—as by the development of yolk-sac placentas in final phases in the growth of embryos, or by the functional modification of either the lining of the oviducts or of the remnants of the yolk-sac or both.

Although arrangements for the nourishment of embryos are usually similar in closely allied forms, they may be different. For example, in the genus *Galeus* (small sharks of the continental slopes), *G. melastomus* lays eggs in leathery cases, whereas *G. polli*, a species of closely similar form, coloration, and even the structure of the reproductive organs, retains the eggs in the oviducts and liberates living young (Cadenat, 1959).

In several species of sharks that produce living young, the method of nourishment of an embryo to bring it to the normal size at birth may include several steps. Each step may involve a change in the manner in which nutrient is delivered to the growing embryo, as in the sandbar shark (Springer, 1960) and the sand shark (Springer, 1948).

The production of young that are especially large in proportion to the length of the mother is neither restricted to one family of sharks nor correlated with the size to which the species grows. Generally, the species that give birth to young especially large in proportion to the size of the mother have small numbers in each litter. The only known gravid example of *Squaliolus* (one of the smallest sharks) was 215 mm in total length and contained three embryos, 87–9 mm long. The sand shark (a large species) never produces more than two young in a season, but Bigelow and Schroeder (1948) mentioned a tiger shark 5½ m long that was said to have contained 82 young. The tiger shark, the blue shark, and the great hammerhead may produce (for sharks) large and widely varying numbers of young in a litter.

The Shark's Position as a Predator

The only important predators of sharks are other sharks, although they have been reported from the stomachs of porpoises and sperm whales and the smaller ones are eaten occasionally by bony fishes. As a group, the sharks occupy in the sea somewhat the same position that man occupies on land: neither is particularly endangered except by others of its kind.

The shark's role in the sea is chiefly that of a predator on comparatively large prey, although two of the largest, the whale shark and the basking shark, feed principally on macroplankton, at least as adults. Other known exceptions are in the Heterodontidae, Orectolobidae, and Triakidae, which are made up principally of small species that feed on invertebrates or small fishes.

Sharks are able to go without food for long periods, during which a huge reserve of fat in the liver appears to be their energy source. The livers of the larger species especially, and of those that feed on large prey, usually account for 10–25 percent of the total weight. The proportion of oil in shark livers varies greatly but may be as much as 80 percent. Among the shallow-water species, at least, the primary advantage of the fat reserve is that it gives the shark wide latitude in times for feeding. It does not greatly affect a shark's well-being to wait for the right conditions for feeding.

The types of prey sought by a shark are no doubt usually of a nature and size best suited to its structural specializations for feeding. So many exceptions have been observed, however, that it seems probable that, in the absence of readily available preferred food, sharks accept a variety of substitutes. A few species—notably the tiger shark, the lemon shark, and the pelagic whitetip shark—are chiefly responsible for the reputation of sharks as scavengers, although all sharks may sometimes eat carrion. The extent of scavenging by sharks is probably magnified in reports of observations because many of the stomachs examined have been from sharks taken in harbors or shipping lanes where waste materials are varied and abundant. Among sharks from the commercial fishery, carrion or rubbish was never a preferred food (Springer, 1963). Preferences for fresh or living food are probably stronger for some species than others, but I suspect that any shark becomes an opportunist in feeding when the proper assortment of stimulating conditions prevail.

Some sharks feed on prey for which they are not structurally adapted. Examples are the whale shark, normally a plankton feeder, swallowing tuna (Gudger, 1941; Springer, 1957); tiger sharks eating large marine gastropods with heavy shells (Springer, 1963); and whitetip sharks taking bites from a compactly balled school of small threadfins, *Polydactylus* (Bullis, 1961). I have found stomachs of a few large silky sharks and spinner sharks packed with small fishes less than 3 inches long and believe that the spinning habit sometimes exhibited by these sharks is a feeding technique used to catch small fishes schooled at the surface (Springer, 1963). The leaping or spinning of other sharks may sometimes be incidental to feeding.

Distribution of Sharks

The geographical ranges of some populations of sharks are intricate and sometimes exhibit shifts in extent over annual or much longer periods. Some sharks, such as the adults of one population of the sandbar shark, may migrate seasonally over long distances (Springer, 1960). On the other hand, seasonal movements by members of other populations may be short—merely the distance required to go from one depth to another; Matthews and Parker (1950) found no evidence of a north-south or south-north migration of basking sharks, although the species appears off the British Isles in early summer and disappears in autumn. Still other populations, especially in regions with little seasonal change in water temperature, appear to be local. Tagging the northern-Pacific spiny dogfish off the coast of Washington showed that one segment of the population of the northeastern Pacific is essentially restricted to Puget Sound, whereas another segment, outside Puget Sound, had a greater tendency to migratory movement (Holland, 1957). Finally, individuals or schools of migratory species may occasionally wander far beyond the normal range of the species.

It will probably be necessary to describe species or population ranges in about the same way that ranges of migratory birds are usually described as knowledge of shark distribution increases. This would require delineating a summer range and a winter range and noting areas of occasional or casual occurrence. An adequate description of shark ranges would additionally require reference to depth distribution in various areas.

Most of my own observations have been made on populations of sharks of inshore waters along the east coast of the United States. Migratory habits are strongly developed here, and the distribution patterns of populations are clearer and geographically more extended than would be expected in an area with lesser seasonal change in inshore water temperatures. A hypothetical life history of a shark belonging to a migratory population of this area is outlined below to show some of the essential features of distribution that appear in rather highly developed shark social organizations.

In this hypothetical population, the young are born in the spring or early summer (each year for some species, in alternate years for others) on specific nursery grounds that are in somewhat shallower water than adults of the population usually frequent. Adult males rarely, if ever, visit the nursery grounds. Females travel either long or short distances to reach the grounds but actually enter the shallower waters of the nursery only when they are gravid and at full term. The females do not feed while on the nursery grounds. They remain in the nursery area only briefly and resume feeding a short time after departure—sometimes at no great distance from the nursery grounds but usually in somewhat deeper water.

The young in the hypothetical population remain in the vicinity of the nursery grounds while feeding and growing to sexual maturity but may move from the area if forced to do so by seasonal temperature changes. Their seasonal migrations are much less extensive than those of adults, but they may form migratory aggregations in winter. These aggregations are made up of members of approximately the same size but include both sexes and usually are not found with or near adults of the species; the separation may be either geographic or bathymetric.

Schools of adults segregate by sex for migration. The schools of males tend to remain in slightly deeper or cooler water than schools of females. In the period between the pupping seasons, these schools of adults often cover a great geographical area—substantially greater than that in which the young are found.

Adult males move inshore in the spring to mate. Periods of temperature inversion often occur along the Gulf coast in the spring, and waters close inshore are often slightly cooler than waters farther offshore. This temperature relation may be a factor in bringing the sexes together in that region.

Thus, in populations of sharks organized as in the hypothetical one, the distribution of the young, of the mature males, and of the mature females differs spatially. Where the total geographical range is extensive, as in the sandbar shark, the difference between the ranges of the adults and young may be considerable. At terminal points of migratory routes, the separation of aggregations of adults may not be distinct except that males do not enter nursery areas.

The degree to which various northwestern Atlantic populations of large carcharhinids conform to the hypothetical one is not uniform. Tiger sharks, for example, show no definite tendency to segregate by size or sex; also, they do not appear to have specific nursery areas separate from the range of adults. Data from the commercial fishery on the other species show differences in the area or times of occurrence of mature males and mature females. Also, specific and more or less restricted nursery areas appear to characterize several of the better known populations. Nursery areas for bull sharks are chiefly in brackish-water estuaries. Young bull sharks are common in summer in brackish-water areas of the northern Gulf of Mexico, especially near the mouth of the Mississippi River, and to a lesser extent in similar situations along the coast of the Carolinas.

Several of the pelagic surface-dwelling species have cosmopolitan distributions in temperate latitudes in both oceans. The large oceanic form generally known as the blue shark has such a distribution, and all blue sharks are usually regarded as members of one species, *Prionace glauca*. Strasburg (1958) has shown that the blue shark in the central and northern Pacific is largely confined to a rather narrow temperature range and shifts its vertical distribution from near the surface in northern latitudes to moderate depths in equatorial waters. He also noted that blue sharks are frequently observed at the surface in the north but never in the tropics. Fewer data are available from the Atlantic, but these data suggest that the distribution there is similar. As Strasburg pointed out, the distribution of the blue shark may be an example of tropical submergence. At least we cannot be sure that blue-shark populations in the northern and southern hemispheres are isolated from one another.

SOCIAL BEHAVIOR OF SHARKS

Definitions

When distinctive responses among members of a group of animals tend to keep the group together, the animals may be said to form a social group. This definition excludes, of course, gatherings in response to other kinds of animals or to objects or conditions in the environment. Etkin (1964) pointed out that a literal interpretation of this definition would include the interaction of the sexes in reproduction and that, in consequence, social behavior may be regarded as universal among vertebrates. Societies of animals exist at many levels of complexity. All have some degree of cooperation among individuals of the same species. Allee (1938) preferred to call the simplest forms "protocooperation" and reserved the term cooperation for relatively advanced forms of group activity. Regardless of the definition used, the idea of animals cooperating in groups seems to be in conflict with the idea that there must be unrestricted and often aggressive competition between individuals to enable natural selection to be fully operative.

Although I see no reason to reject the broad definition of a social group given above or even to object to narrowing or restricting the meaning in application to the study of some animals, I find it inconvenient to use it as a starting point in an account of the shark social organization. Little information exists to show that territoriality is or is not involved in the shark social organizations, and even less information exists to indicate a dominance hierarchy. Nevertheless, some shark populations exhibit complex behavior that constitutes a part of their social organization.

The degree of development of social behavior varies greatly among sharks, and a broad definition of a society is needed to apply to sharks generally. An excellent one was supplied by Wynn-Edwards (1965) who defined a society as an organization of individuals that is capable of providing conventional competition among its members. This definition is sufficiently broad to include the simplest of animal societies and is expecially apt for sharks in drawing attention to one of the primary functions of a society—the regulation of intraspecies competition so as to permit natural selection to operate without excessive waste. Sharks were not considered by Wynn-Edwards in reaching his definition, possibly because the general literature on social behavior of animals contains little, if any, reference to sharks. Probably the folklore flavor of much of the general information available on shark behavior has left sharks in limbo for much scientific consideration of the nature of their social arrangements. Data have gradually accumulated, however, from experimental studies of shark behavior (e.g., Clark, 1959; Gilbert et al, 1964; Tester, 1963; Wisby et al, 1964; to mention only a few recent studies) that not only add to the backlog of information on sharks but also give promise that we will have a constantly improving understanding of the physiological basis for their behavior. Since we now have Wynn-Edwards' useful definition of a society, it seems worthwhile to take a first look at the social organizations developed by sharks.

Types of Observations of Social Behavior

Observations from airplanes, in particular, indicate that large sharks (and rays) are often in groups and not randomly distributed. Such groups, in close array, that I have seen on several occasions included single-species aggregations of sandbar sharks, silky sharks, great hammerheads, tiger sharks, spinner sharks, and blacktip sharks; all appeared to be migrating or wandering in social groups not brought together by some transitory environmental phenomenon. Clark (1963) described a huge aggregation of cownose rays estimated from an aerial photograph to consist of 3,000–6,000 individuals.

Many observations of groups of sharks moving in close association have been made but not reported in the literature. No doubt a few such groups are aggregations that have assembled from a scattering of individuals solely because of the presence of food, but certainly many of them are not so formed. Some groups are far too large to have assembled from a population resident in a small area, and some apparently are not feeding when observed but appear to be wandering or migrating. Perry W. Gilbert (personal communication) described an aggregation of over 200 large sharks (2–4 m long) observed off Miami, Florida, from a helicopter. He stated that one group of 15–20 large sharks formed a head-to-tail circle about 50 feet in diameter and milled about during the 15–20 minutes that they were under observation.

Aggregations of sharks that appear around vessels, anchored or adrift while fishing, are probably not, as a rule, social groups. Frequently, sharks gather around a boat because of the presence of food, such as chum or bait, or merely because the vessel represents a new element in the environment. Limbaugh (1963), referring to dozens of *Carcharhinus galapagensis* that surrounded his boat at Clipperton Island, noted no evidence of schooling or coordinated behavior.

Direct observations of sharks in nature have furnished few clues to their social organization beyond the fact that they occasionally appear to travel together in groups made up of individuals of nearly equal size. Such observations as have been recorded suggest that the larger species assemble in smaller numbers than do the smaller species, as might be expected because of the lower population density of the larger forms.

Much more information pertinent to the social organization of sharks can be developed from their temporal and spatial distribution as shown by catch records of research vessels and of commercial fishermen who keep comprehensive records of catches. The most useful information concerns the distribution of shallow-water sharks along the Atlantic coast of the United States, where the annual change in water temperature is sufficient to involve all of the commoner species in north-south migrations. This migration is complicated by the presence of warmer and less variable Gulf Stream water offshore and on the outer reaches of the continental shelf off the Carolinas. The latitudinal ranges of sharks of the area are greatly extended. The result is that differences in geographic range or habitat preference (or both) of sexually mature males, sexually mature females, and immature stages are so greatly magnified that they can be estimated from catch records. The migration of the sandbar shark was described in an earlier paper (Springer, 1960) based in part on these records. In later discussion, I shall draw heavily on unpublished shark-fishery records and on my own notes of field observations.

Mating Behavior

In all elasmobranchs, mating requires the introduction of one or both claspers into the cloaca and oviduct or oviducts of the female. The claspers of sawfishes and some other rays are too far apart to permit their simultaneous use, and some rays (for example, stingrays) have only one functional oviduct (Gilbert, 1958). Possibly the alternate use of claspers is the rule among elasmobranchs. In the sharks, all known species have two functional oviducts, but occasional gravid females have been found with developing embryos in one oviduct and infertile eggs in the other. This condition is rare in the smaller species but frequent among the larger species of *Carcharhinus*. Whether fertilization of only a part of the normal complement of eggs is due to mating in which only one clasper is used is not certain, but the tendency to a lowered fecundity among large species of *Carcharhinus* is most easily explained by the greater mechanical difficulties in the large species with minimal body flexibility. Among the larger species, some cooperation on the part of the female seems necessary.

The few recorded observations of mating include little on courtship; most concern small sharks or rays and do not mention activities or displays that really merit the term courtship. The mating of the clearnose skate described by Libby and Gilbert (1960) may be characteristic of the mating of many of the smaller species of sharks and rays. In the action observed, the male seized the female by biting the pectoral fin, and mating followed.

Special modifications of the teeth of males have developed in a few species of small sharks, seemingly to make grasping more effective. The teeth of relatively few species of sharks show sexual dimorphism. The teeth of some male squaloid sharks, notably in the genus *Deania* (Cadenat, 1960; Garrick, 1960), are more erect than the teeth of females and should function more for holding than cutting. Among scyliorhinids, the sexually mature males of *Halaelurus chilensis* and *H. bivius* have longer teeth with fewer cusps than females. The most extreme dimorphism known in the teeth is in *Apristurus riveri*, a small scyliorhinid of the lower continental slopes of the Caribbean Sea. The teeth of mature males are about twice the length of teeth of females of the same size, and they also differ in shape; the males have teeth consisting of a single conical cusp instead of the somewhat flattened 3- to 5-cusped teeth characteristic of the females.

Among the larger carcharhinid sharks, indirect evidence from captured sharks suggests that the males harass the females persistently and violently to induce cooperation in mating. Cooperation by the female is essential in mating because the jaw armature of the males is such that the male probably could not bite and hold the female without producing a very severe injury. Furthermore, it seems probable that the trunk region of males is not sufficiently flexible to hold the females during mating. The harassment of females during the mating seasons is a form of courtship continuing sometimes for long periods.

Minor cuts and scars, interpreted as courtship injuries, are common on mature females of the larger species of carcharhinid sharks, especially those having flattened, triangular teeth obviously effective for cutting. The distribution and number of scars vary somewhat, although they usually are most numerous on the dorsal surface of the pelvic region. Typically, they seem to be produced by short slashes that do not show the imprint of several teeth or the crescentic pattern of the jaw. Characteristic courtship scars on blue sharks in the Pacific Ocean were illustrated by Suda (1953). A correlation between the presence of fresh and only partially healed cuts and the appearance of early embryos was noted in the sandbar shark (Springer, 1960).

Minor cuts and scars are rare on males, and such evidence of injury to males as does appear is usually restricted to dismemberment—cut-off fin tips or claspers. I have not seen sharks with healed scars of major bites that removed substantial amounts of body skin and muscle tissue, and assume that these bites are usually lethal.

Courtship scars are generally not evident on the smaller species and cannot be detected by ordinary examination of sharks that have long spike-like teeth. These scars were a problem, however, in leather production from large sharks in the commercial shark fishery in Florida before 1950, when hides were an important source of revenue. Preliminary grading of the hides was necessary to avoid expensive tanning of hides with scar tissue, because deep scar tissue produced holes in the leather. Hides of all large female sand sharks (a species with spike-like teeth) had to be discarded because of pinholes, whereas the hides of large males were generally satisfactory. This difference turned our attention to the much more frequent presence of minor scars on females of other species such as tiger sharks, sandbar sharks, dusky sharks, and bull sharks, and the great scarcity of scars in the males.

On the basis of present knowledge of the large carcharhinids of the Florida region, it seems that the males are restrained by conventional behavior in courtship merely to slashing a bit in an attempt to induce cooperation. Springer (1960) reported on some indications that male sharks may not feed during courtship but that the females do. Courtship thus becomes a hazardous activity for the males of some of the larger species since they are inhibited from strong attack, whereas the females may sometimes respond by killing the males—an act that is aided perhaps by the fact that, on the average, the nongravid females outweigh the males by 25 percent or more.

Only once was I reasonably sure that I had obtained both members of a mating pair of tiger sharks soon after mating. This occurred at Englewood, Florida, on 27 May 1938. The female was collected from a longline set in water shallow enough that the sharks on the line were visible from the surface. A male which was not hooked accompanied the female at a distance of only a few feet and even came to the surface while the female was brought aboard the boat. The longline was left in place, still with bait on some of the hooks. After the female was brought ashore, she was found to bear wounds believed to be characteristic of courtship. We returned to the line in an hour and found that the male had taken a bait. Vascular swelling at the base of the claspers, the presence of sperm cells in the seminal vesicle, and sea water in the clasper siphons indicated that it had recently copulated. The male was undamaged externally but was extremely thin and had a dark, nearly oil-free liver weighing less than 10 lb—about 10 percent of the usual liver weight for a male tiger shark of its length (4 m). The decrease in liver size suggested a long period of fasting for this shark during the mating period.

My observations as a commercial shark fisherman were directed especially to the condition of the livers. Although reduction in liver size in presumed postnuptial males from the species-average was not consistently great, it usually was substantial. This reduction in oil content increased the value of the liver by concentrating the vitamin A in a smaller amount of oil.

I made many observations on the postnuptial condition of large male sharks in 1935–50 in the Florida-Gulf of Mexico area that were similar but less detailed than the one just described. Circumstantial evidence indicated that sharks with fully developed and bleeding claspers, greatly enlarged testes, filled seminal vesicles, and more or less extensive edema around the base of the claspers were either in the mating cycle or had recently mated. These criteria were also noted by Clark and von Schmidt (1965) as indications of the mating season and postnuptial condition.

Segregation by Size and Sex

The tendency for elasmobranchs to associate in groups of individuals of about the same size is general, although exceptions appear occasionally, especially among the smaller species. The general tendency also exists, but with more exceptions, for the adults to segregate by sex. Apparently the tendency for sharks to assemble in large but somewhat diffuse groups is stronger during migration and weaker at terminal points of migratory routes. Segregation of adults into schools made up predominantly of one sex also seems to characterize the migratory populations to a greater extent than the nonmigratory ones.

Migrations of sharks are greatly influenced by seasonal changes in water temperatures, but other factors contribute. Migrations take sharks to rather specific places or environments where the females lay eggs or give birth to young and probably also to other more or less specific areas where mating occurs. The evidence of the existence of special nursery areas for some sharks is rather strong, but the evidence for specific mating areas is tenuous.

For all well-known, shallow-water sharks, the young tend generally to concentrate in the shallower parts of the range of each population and near nursery areas. Where migrations occur, the distances traveled by the immature individuals seem to be appreciably shorter than those traveled by the adults (especially gravid females).

In treating segregation by size as a social phenomenon, it is recognized that schools of sharks in migration might be sorted into different size categories by differences in swimming speeds between the smaller and larger individuals. Segregation by size might also result from differences in habitat and food preferences between large and small sharks. Observations that small sharks actively avoid larger sharks, however, suggests that an element of choice is present and that, in part, segregation by size is social.

Details of the distribution differ somewhat in different populations, but the tendency to segregate by size and sex has been noted in many of the more comprehensive studies of shark population distribution (Ford, 1921; Hickling, 1930; Templeman, 1944; Ripley, 1946; Olsen, 1954; Springer, 1960). Local segregation of adults by sex has been observed commonly in the commercial fishery, although it is not always apparent from examination of catch records because groups made up primarily of one sex are sometimes found near groups of the other sex. Perry W. Gilbert (personal communication) found adult male spiny dogfish in July and August in small groups, isolated from the females, in Frenchman's Bay, Maine. The two groups did not seem to mix.

The populations of well-known sharks of the shallow waters of the northwestern Atlantic show several levels of complexity in social organization with respect to the use of restricted nursery grounds that are more or less free from large sharks of any species. The tiger shark and the nurse shark appear to be at the lower level of social organization; the lemon shark, the smooth dogfish, the spiny dogfishes, and the hammerhead sharks seem to be at various intermediate levels; and several species of *Carcharhinus*, the sharpnose shark, and the sand shark are at the highest level.

Female sandbar sharks of the northwestern Atlantic population usually do not feed while in the principal nursery areas (Springer, 1960). Some other species of *Carcharhinus*, as well as the smaller sharpnose shark in the northwestern Atlantic, have similar habits. Evidence tying together the facts of distribution with habits is difficult to assemble because questions of identity of species have only recently been settled to the point where distributional data are reasonably reliable.

The principal nursery areas of the bull shark in the northern Gulf of Mexico are the shallow, brackish-water bays and estuaries. The newborn young are easily taken there in midsummer on baited hooks. At the same time, large bull sharks are very common in the deeper and more saline waters at depths of 10–35 m, where they are the most abundant species taken on baited longlines. Large bull sharks are not taken on baited hooks in the shallow brackish areas, although adult females have been observed in the late spring. I have been unable to elicit any aggressive response from them in spite of prodding and pushing while in the water beside them. In defense of my sanity, I should point out that I did this long ago when I did not believe that sharks attack man.

Requirements for nursery grounds for some species other than the sandbar shark and the bull shark may be exacting as to the depth of water and the kind of habitat, but, at least in the tropics and away from the shore line, the grounds may be widely scattered geographically. Thus, nursery grounds for the silky shark in the north Atlantic-Gulf of Mexico-Caribbean area (as shown by the capture of newborn young) are at the bottom along the outer rim of the continental shelf, often at depths of 80–100 m and frequently in areas where red snappers (Lutianidae) are caught. Additional nursery areas for the species are on oceanic banks such as Serrana Bank in the western Caribbean.

A general view of the distribution and relative abundance of the species of sharks in continental-shelf waters suggests that the availability of nursery areas, not only suitable to each species but also comparatively free of predation by larger sharks, is very important in interspecies competition.

Feeding Behavior

In the most common shark-feeding behavior, the initial attraction to food is frequently olfactory, although it may also be auditory or occasionally even visual. Whatever starts the feeding response, other stimuli may appear to reinforce it, including probably some reinforcement from an initial success in obtaining an acceptable morsel to swallow. The aspect of greatest interest in this discussion is that the rate of feeding is likely to increase progressively with an increase in the number of sharks present.

Shark feeding appears to be an automatic process that always starts slowly and gathers momentum if a series of feeding stimuli occur. The solitary shark, predisposed to feed for whatever reasons, moves about investigating the environment, sometimes testing objects by bumping them with its snout. Occasionally, it makes short dashes after prey and, whether successful or not, returns to a leisurely inspection of the area. If another shark of similar size appears, setting up the possibility of competition for food, the bumping of inanimate or slow-moving objects is discontinued and these are taken into the mouth for testing. When food is found, especially when more than one shark is present, the rate of swimming and attack by all members of the group increases. If the prey is large, and if its struggles produce a commotion in the water, the tempo and ferocity of the attack increase further.

It is clear from observations in the field and experiments with sharks in tanks that olfactory and visual cues play a part as stimuli that cause sharks to feed and that vibrations and noise (however perceived by the shark) have important roles as feeding stimuli. I find no indication, however, that the kind of internal drive that men know as hunger operates or even exists for sharks. I have no evidence to offer that a hunger drive does not exist for sharks, but suggest that it may play a minor role acting perhaps at a nearly constant but low level. My chief reason for suspecting that hunger is not very useful in describing the shark's urge to feed is that in the commercial fishery the best and largest catches I have seen were of sharks with stomachs partly or nearly full of freshly eaten fish, turtles, and invertebrates, not obtained from baited hooks, whereas poor catches included, for the most part, sharks with empty stomachs.

The disposition of sharks to feed may be variously inhibited by circumstance or conditions in the environment. A shark newly placed in a tank is probably less disposed to feed than one in a familiar environment to which it has become adjusted.

Essapian (1962) noted difficulty in getting sharks to feed in captivity at the Seaquarium, Miami, Florida, and at Marine Studios, St. Augustine, Florida, but twice observed very brief periods of attacks on fishes in tanks with the sharks. Springer (1954) observed flurries of feeding among groups of four to six captive smooth dogfish usually lasting only one or two minutes during the testing of shark repellents.

Bigelow and Schroeder (1953) noted that fishermen describe feeding by the spiny dogfish as being like that of packs of dogs. Migratory schools of dogfish sweep through an area, feeding as they go. From the many observations by fishermen, it appears that aggregations may be very large and rather loose, with individuals widely scattered until favorable concentrations of food are encountered.

Possibly similar dog-pack feeding is carried out by a related but much smaller species, the green dogfish. This species occurs abundantly on the northern coast of the Gulf of Mexico—most commonly in depths of 350–400 m. The adults are about 25 cm long. Like some other members of the genus, this species has an elaborate and distinctive pattern of photophores. Repeated drags of trawls in the same depth and habitat usually catch many or none, suggesting that the species occurs in rather dense aggregations. Contents of hundreds of stomachs showed that more than half their food is squid or octopus. The cephalopod beaks and eyes commonly found in their stomachs were often so large that shark's jaws and gullet must have been stretched greatly when the parts were swallowed. I deduce that green dogfish hunt in packs and may literally swarm over a squid or octopus much larger than they are, biting off chunks with the razor-sharp band of lower-jaw teeth and perhaps maintaining the integrity of their school visually through their distinctive lighting system.

In the commercial shark fishery centered at Salerno, Florida, 1935–50, it was found by study of the catch records over a period of several years that fishing success depended upon concentrating the initial attraction of sharks to the baited hooks on bottom longlines. The fishing-company management, acting on the assumption that shark feeding was difficult to initiate, persuaded fishermen to use methods that would hook the first shark as soon as possible after a line was set. It was believed that the commotion on the longline produced by a hooked shark attracted others. Fishermen following this principle greatly increased their catch per unit of effort.

Sharks hooked by fishing gear are subject to attack by other sharks in areas where sharks are numerous. Off the Mississippi River passes, for example, substantial portions of shark catches left overnight on set lines are damaged or eaten by other sharks which may themselves be caught in the process. Foumanoir (1961) reported that, in captures of cowsharks off the Comores Islands at night, specimens caught on hook and line were often followed and harassed all the way to the surface from 150–200 m by other cowsharks and that about a third of the cowsharks caught bore toothmarks, apparently made by other cowsharks.

Stomach contents give ample evidence that sharks eat other (usually much smaller) sharks. Although all of the species having jaws with teeth suited to predation on large prey probably eat other sharks when the opportunity offers, some appear to obtain a substantial portion of their diets through predation on smaller sharks. The white shark, the dusky shark, the tiger shark, the great hammerhead, and the bull shark, taken by the Florida commercial shark fishery, frequently had shark remains in their stomachs that had not originated from attacks on sharks already hooked. This list includes the five largest and heaviest predatory sharks found in the inshore waters of Florida. One of these species, the bull shark, apparently has a decided preference for sharks as food. Near the mouth of the Mississippi River, mature bull sharks (which may weigh as much as 500 lb) feed extensively on adults of the smaller species common in the area—notably the sharpnose shark, the smalltail shark, the bonnethead, and the blacktip shark—at least to the extent that these sharks are present in depths of 5 m to about 35 m. If these small species move farther offshore into deeper water, they are likely to be the victims of tiger sharks or dusky sharks, and if they try middle and surface layers they may be eaten by hammerheads.

One species-group to which the bull shark belongs, called the *Carcharhinus leucas-gangeticus* group by Garrick and Schultz (1963), is especially predatory on smaller sharks. One member or another of this species-group is common inshore along all tropical and warm temperate continental coasts and the coasts of some large islands. It is abundant near the mouths of the larger rivers. Adults are 2½–3½ m long and are comparatively heavy for their length. Aggressive action against other sharks was demonstrated in a 46-foot-diameter exhibition tank by a member of this group taken off Natal. (The species is common there and is locally known as the Zambezi shark; see D'Aubrey, 1964.) Davies (1964) reported that one 240-lb Zambezi shark ate several other sharks in the tank with average weights of 10 lb and attacked larger ones even though it fed on tuna daily. Although not all of the Zambezi sharks introduced into the tank behaved in this way, the species clearly takes aggressive action against other sharks.

A distinction probably should be made between the kind of behavior involved when a large shark, acting alone, swallows a small shark with one or two bites and kinds of behavior that are merely an assertion of dominance. This distinction is not always clear, however. I have observed actions between two species that might be regarded as showing dominance when whitetip sharks were feeding near a vessel at the surface in company with silky sharks, in a mixed aggregation in which all individuals were of about the same length. When competition for a tidbit was between a whitetip and a silky shark at close quarters, the silky shark gave way to the whitetip shark, but, when the competition was between two whitetip sharks or between two silky sharks, both appeared to close in on the food without reluctance even though some physical contact or buffeting resulted.

Observations suggest that feeding schools of small sharks give way to individuals or schools of larger sharks. Both commercial fishing experience and observation suggest that hammerheads have a special status, because sharks of other species tend to stay at a distance from them even when no great disparity in size exists. Possibly the hammerheads have an advantage over other species in fighting because of superior maneuverability given them by use of the broad plane of the head as a forward rudder.

The Feeding Frenzy

The feeding frenzy has been reported frequently. It is all that the name implies and is characterized by extreme savagery of attack in feeding; the sharks move at an accelerated speed and exhibit a total disregard for any injuries they may receive in the attack. The intensity of the feeding frenzy may vary, but apparently its more extreme manifestations are not common. Apparently, feeding frenzies develop only when a series of strong feeding stimuli occur under conditions that are otherwise favorable for shark feeding. My own experience suggests, for example, that these occurrences are more common at the surface on moonless nights, for I have heard far more of them than I have seen. Groups of sharks appear always to be involved, apparently with the intensity of the frenzy in direct proportion to the number of sharks present in the immediate vicinity. The most interesting aspect is that at the height of excitement of the sharks any injury to one of the sharks may cause the others to turn on the injured one and devour it.

Vorenberg (1962) was able to induce a series of shark-eat-shark episodes involving 2- to 3-m lemon sharks and bull sharks in the Lake Worth, Florida, estuary but only under specific conditions. The episodes developed only at night, in the absence of bright moonlight, on an outgoing tide and after some preliminary excitement had been generated. Furthermore, the active participation of more than six lemon sharks or bull sharks, or both, was required. When one of the sharks finally got the bait and was hooked, the other sharks turned on it and devoured it.

I have observed one feeding frenzy involving a large number of sandbar sharks (perhaps as many as 200) in which several members of the school of sharks were eaten by others in the school. The action was so rapid that it was impossible to determine whether the victim was already injured and bleeding prior to its destruction. Each instance followed a collision of two or more sharks brought about by their simultaneous arrival at pieces of charcoal that were tossed from our vessel into the midst of the wildly excited school.

Summary of Social Conventions of Sharks

From the foregoing accounts, only five distinct social conventions emerge: (1) the more or less universal tendency to segregate by size, (2) the tendency among some species for sexually mature individuals to segregate by sex except during mating seasons, (3) the development of feeding inhibitions by males during courtship among the larger species with formidable jaw armature, (4) the habit of gravid females at full term to stop feeding while on the nursery grounds, and (5) the use by some species of special nursery grounds outside the normal geographical or habitat range of sexually mature males. These rather simple conventions are most obvious in the populations of the larger species of carcharhinid sharks that carry out extensive migrations.

The most widespread social convention among sharks is their tendency to segregate by size. The habit apparently is more or less universal among species that are reasonably well known. The shark's strong tendencies to predatory aggression make segregation important for survival of the species.

The degree to which species of sharks form separate schools of adult males and adult females varies greatly, but apparently segregation by sex is closely related to the need for special nursery grounds for the migratory and predaceous species that produce only a few comparatively large young. Adults of the tiger shark, a less gregarious form than most of the other well-known inshore species, are not known to form sex-segregated schools.

Inhibition of feeding by the males during courtship and by females during parturition occurs in a few species of carcharhinids, but little is known of the prevalence of such a habit in other families.

Interspecies competition for suitable nursery grounds appears to be severe and particularly important to the carcharhinid and hammerhead sharks that dominate the inshore waters in the tropics and the warmer temperate seas. Competition for nursery grounds between the population of bull sharks and the population of sandbar sharks in the northwestern Atlantic is indicated by the circumstantial evidence of distribution (Springer, 1960), but less specific evidence is available about competition among other populations of the area.

To learn more about the social organizations among shark populations, we not only need more observations on sharks but also more information on shark distribution. We also should put greater emphasis on records of environmental data and on the inclusion of negative information. It is important to know about the absence of an animal as well as about its presence. Since some sharks do not ordinarily take baited hooks and many live in relatively inaccessible places, the collection of full information on their distribution presents a real challenge.

SOME SPECULATIONS ON DENSITY-DEPENDENT POPULATION CONTROL

Food Supply and Population Density

Immature and female sharks of the shallow-water populations of the Florida-Gulf of Mexico-Caribbean region have uniformly plump livers containing a high proportion of oil. Exceptions must exist, but I can recall seeing only a few in some thousands of sharks examined (all were unusually large examples of the great hammerhead, which had indications of senility—atrophied ovaries). Among sexually mature males, thin livers with a low oil content are frequent. It is postulated that this condition and the general tendency for mature males to have livers with a higher concentration of vitamin A are due to prolonged fasting during periods of courtship—periods of irregular duration but often considerably longer than the fasting period of females at the time of parturition.

If we accept the proposition that sharks with plump livers that contain a high proportion of oil are well fed, we must conclude that sharks usually have little difficulty in finding enough food, despite annual or seasonal fluctuations in the supply. This conclusion conforms to the view expressed by Bodenheimer (1958) that selachians, along with some other catholic predators, always find food in sufficient quantities to meet their needs. The implication must follow that some factors other than food supply hold populations of sharks at some point below the level of the maximum population density that could be sustained by the available food supply.

In the warmer shore waters, such as those off the Florida coasts, the geographical and habitat ranges of sharks form an overlapping mosaic in which the ranges of adults and young usually are separated, at least by habitat. In this area, the entire group of species appears to constitute a single interacting system, not only in competition for food but also in competition for nursery areas. Here, sharks may compete with one group of species when immature and a different group when mature. Although feeding habits and food preferences differ somewhat among species, the difference is usually not great between individuals of equal size. Thus, competition for food is primarily among sharks of similar size rather than among members of a single species.

Local fishing efforts in warm-water, near-shore areas appear to reduce the availability of sharks in the locality but only as long as the fishing effort is maintained. The only substantial change in the abundance of large sharks apparent from the records of the Florida commercial shark fishery occurred in the spring and summer of 1937 when adult bull sharks appeared in such great numbers along the southeastern coast of Florida that facilities for handling the catches were inadequate. The catches of bull sharks in relation to the catches of other species returned to normal the following year, and catches continued without major fluctuation until the fishery closed in 1950. I could find no evidence of a change in food supply during the 1937 season and suggest that the phenomenal increase in numbers of bull sharks occurred because a segment of the migrating population that would normally be headed toward the northern Gulf of Mexico from the Florida Keys region was in some way diverted to the Atlantic coast of Florida.

Competition between species of sharks becomes less important away from the warm-water, near-shore environments that support many kinds. Here, fluctuations in abundance or year-to-year changes in distribution that affect local population densities seem to be more frequent. Presumably, these changes are the result of climatic factors that act directly or affect the food supply. Because sharks are long-lived (at least in cool-water environments) and reproduce at a comparatively slow rate, it should be expected that naturally occurring changes in actual population abundance would be slow. Furthermore, it would be expected that such populations would be especially vulnerable to intensive and prolonged fishing pressures. The effect of fishing pressures is sometimes clearly apparent. Examples of reduction in abundance due to fishing pressure were noted for the northwestern Pacific population of the spiny dogfish in 1940–50 (Alverson and Stansby, 1963), for the soupfin shark in 1941–49 (Ripley, 1946), and for the Australian school shark in 1941–44 (Olsen, 1954).

Changes in abundance not related to fishing have been observed but are not so well documented. Apparently, however, periods of higher and lower abundance of the northeastern Atlantic population of the spiny dogfish, noted by Bigelow and Schroeder (1953) as based on reports of fishermen, were not related to fishing pressure. It is interesting to note the two periods of high abundance on the New England coast that appeared about 55 years apart. The first observed period of peak abundance on the New England coast was in 1904–5, after a build-up in population strength extending back 20–30 years. By 1913, the population had decreased considerably, and until recently the population level seems to have been comparatively low. Beginning about 1961, however, fishermen on the New England coast again became especially concerned about an apparent increase in the numbers of dogfish.

Self-Regulating Mechanisms Operating in a Complex of Shark Populations

Several shark populations interact competitively in the continental-shelf waters off Florida and in the Gulf of Mexico. Here, I can discuss only the group of populations of sharks belonging to the closely related Triakidae, Carcharhinidae, and Sphyrnidae that are either permanently or seasonally in the Florida-Gulf of Mexico region. In this area, a large number of species are considered as members of a single complex, related through predation on one another and competition for food.

Of the total shark fauna of the area, all are members of the suborder Galeoidea except the spiny dogfish, which occurs only seasonally and irregularly off the northeastern coast of Florida, and one or more species of angel shark, found on the outer continental shelf in the northern Gulf of Mexico and probably also off northeastern Florida. The galeoid sharks of the area include, in addition to the families mentioned above, one of the Orectolobidae, the nurse shark, that does not appear to have any important competitive relation with other sharks of the area; one of the Isuridae, the white shark, a predator on other sharks but relatively rare in the region; and one of the Odontaspidae, the sand shark.

The sand shark is excluded from the group of species to be discussed because its feeding habits differ somewhat from those of carcharhinids (it is not known to eat other sharks), and little is known about its distribution or abundance in the area concerned. The remaining 21 species of the area are divided here for convenience into two groups: 8 are small species that mature at a length of less than 175 cm, and 13 are large species that mature at lengths greater than 175 cm.

Both large and small species have definite nursery areas that are restricted as to habitat type and depth of water. The more productive nursery areas of each species apparently are also somewhat restricted geographically. Nursery areas for the tiger shark, if they exist, are not defined but presumably are close inshore.

The smaller species at all ages appear to be subject to rather heavy predation by larger species, but evidence is scant that larger sharks prey on individuals more than 175 cm long except in areas of high density (as, for example, near the Mississippi River passes in summer).

I have found no evidence that any of the small species become involved in a feeding frenzy in which they damage or kill one another. Probably the smaller species have insufficient weight or jaw strength to make lethal attacks on other sharks of their size. Sharks of the smaller species only occasionally had remains of other sharks (always much smaller than themselves) in their stomachs.

The abundance of smaller species appears to be subject to great local variation even during seasons in which they would be expected to be present in numbers. Periods of relative scarcity in an area may last for several years and are followed by periods of apparent increase.

Fragments of data on the sex ratios of some of the larger species and a few observations on the proportions of populations represented by gravid females suggest that low fecundity may be a factor in the control of population size. In the sandbar shark, I found a higher proportion of nongravid females in the commercial catch than would be expected (Springer, 1960) and also noted that gravid female dusky sharks, a larger species than the sandbar shark, often had embryos in only one of the oviducts, suggesting some difficulties in mating. I advanced the hypothesis (Springer, 1960) that the high ratio of females to males, which was about five to one in a sample of the sandbar shark population, was due to a difference in mortality of the sexes. A high proportion of females to males in catches of the sandbar shark was also noted by Clark and von Schmidt (1965).

My interpretation of the foregoing observations is that each of the 21 large and small species of sharks in the Florida-Gulf of Mexico area is represented by a population that is subject to density control through interaction among the species of the group. The social organization of each of the populations is somewhat similar to the others. Each population is influenced to varying degrees by all of the other populations, and collectively they form a single interacting system. The system cannot be described completely because, at the periphery of the arbitrarily selected area, there is further overlapping with other populations rarely or never present in the selected area.

In the section of the shark world being considered, it seems that the smaller species are held considerably below the density level the area could support by the predation of the larger sharks of the system. The larger species are the ones that in effect supply most of the self-regulation that exists. Density-dependent mechanisms of apparent importance for a single species among the larger sharks include accidental predation in feeding frenzies and possibly, for some species, a reduction in fecundity due to mortality to males during courtship. A limiting factor effecting the total population of the entire system may be the availability of suitable nursery grounds that are small in area and may be insufficient to support larger numbers of sharks. Young sharks forced to leave nursery areas prematurely because of inadequate food supply would presumably move into areas where predation would be severe.

Summary

Social organizations exist at several levels of complexity among populations of sharks. In populations with the more highly developed social organizations, segments of populations made up of sexually mature females, sexually mature males, and immature sharks of both sexes are separated during the greater portion of the life cycle; each segment occupies a more or less distinct geographical or habitat range during a substantial portion of each year.

The tendency toward segregation by size is almost universal among sharks. Under normal circumstances, sharks of approximately equal size show little aggressive action toward one another. Little is known about the internal relationships of groups of sharks, but no indications have been observed of the existence of hierarchies within groups of sharks of the same species. Feeding aggregations of groups of mixed species have been noted frequently, but these aggregations are generally made up of sharks of approximately the same size or show some spatial segregation of size groups.

Segregation by size is a basic feature of the shark social order: it has the obvious advantage of reducing predation on small sharks by larger ones of

the same species. Whether size segregation is brought about in part by factors other than responses of individuals to one another, as by differences in swimming speed, is not important in the final result.

Because most sharks are indiscriminate predators—the larger ones feeding on smaller ones, especially when the disparity in size is considerable—the young of some species are produced in specific nursery areas that are more or less free of much larger sharks of any species, thus giving the young a better chance for survival.

The value of these nursery areas is enhanced by the habit of females of some species to stop feeding at the time of parturition. The period of feeding inhibition is brief and includes only the time required for the females to enter the nursery area, deliver their young, and leave.

The sexually mature males are aggressive toward females during mating seasons and induce cooperation of the female in mating by biting or sometimes (in the smaller species) by holding with the jaws. Among the smaller species of sharks, a few exhibit sexual dimorphism in the teeth; the teeth of the males in one species are twice the size of the teeth of the female and much modified in shape so that they are better adapted to holding than cutting. No tooth dimorphism exists among the larger species with formidable cutting teeth. In these large species, the adult females are sometimes severely slashed and scars of courtship are frequent.

During active courtship, the males do not feed and apparently are inhibited from biting females in such a way that permanent damage is done. Apparently, males stop feeding only in the actual presence of receptive females and may resume feeding as soon as they are separated from the females by a considerable distance, perhaps a few hundred meters.

The courtship of the larger species with cutting teeth is probably a period of peril to both sexes but especially to the males. The females show no evidence of inhibitions to feed during courtship. Since the females usually are somewhat larger than males, among the larger carcharhinids at least, retaliation by females presumably could cause the death of the male.

The importance of hunger as a factor in initiating feeding by sharks is questioned. Field observations suggest that initial stimuli sufficient to induce sharks to feed must be comparatively strong ones of external origin and that the speed and intensity of feeding activity may be variously reinforced by other stimuli including that afforded by competition for food. In some situations of high shark density, this competition may lead to severe mortality, as sharks in a feeding frenzy kill and eat other sharks of similar size.

In an arbitrarily defined area in the Florida-Gulf of Mexico region, where a large number of sharks exist, the geographical and habitat ranges of 21 species overlap in a complicated mosaic. In such a situation, the immature sharks of a population of one species may be in competition with one group of shark species while young but with a different group of species as adults.

The hypothesis is advanced here that the group of sharks in the selected area makes up a segment of a single interacting system of many species of sharks. The general success of the larger sharks in this system is regulated by strong interspecies competition for nursery grounds. The numerical abundance of the total complement of the larger species in the interacting system is regulated also by internal density-dependent controls acting variously within the different species but chiefly affecting the most abundant and more social species through reductions in fecundity and attrition in group feeding. Both reduced fecundity and attrition in feeding are more likely at high population densities. The numbers of the smaller species in the selected area are held in check by predation of the larger species. The system operates to hold the numbers of the smaller species in a rough balance. The numbers of the larger species fluctuate little from year to year, although local anomalies of distribution may produce temporary concentrations at a higher than usual level.

The example used was from a region apparently favorable to sharks and one that supports a large and varied fauna. The populations of sharks within the boundaries of the region certainly interact with sharks outside these boundaries to form extensions of the mosaic of distribution. Somewhere toward the periphery of the range of the total shark fauna, in very deep water or toward the Arctic or Antarctic regions, the environment becomes less favorable to sharks, the number of species present is reduced, and the interaction of populations of sharks becomes progressively less important.

Common Names of Sharks and Batoids with Scientific Name Equivalents

Angel shark	Family Squatinidae
Atlantic spiny dogfish	*Squalus acanthias acanthias*
Australian school shark	*Galeorhinus australis*
Basking shark	*Cetorhinus maximus*
Blacktip shark	*Carcharhinus limbatus*
Blue shark	*Prionace glauca*
Bonnethead	*Sphyrna tiburo*
Bull shark	*Carcharhinus leucas*
Clearnose skate	*Raja eglanteria*
Cownose ray	*Rhinoptera bonasus*
Cow shark	*Hexanchus griseus*
Dusky shark	*Carcharhinus obscurus*
Great hammerhead	*Sphyrna mokarran*
Green dogfish	*Etmopterus virens*
Hammerheads	Family Sphyrnidae
Horn shark	*Heterodontus francisci*
Lemon shark	*Negaprion brevirostris*

Marbled catshark	*Galeus arae*
Nurse shark	*Ginglymostoma cirratum*
Pacific spiny dogfish	*Squalus acanthias suckleyi*
Sand shark	*Odontaspis taurus*
Sandbar shark	*Carcharhinus milberti*
School shark	*Galeorhinus australis*
Silky shark	*Carcharhinus falciformis*
Sharpnose shark	*Rhizoprionodon terraenovae*
Smalltail shark	*Carcharhinus porosus*
Smooth dogfish	*Mustelus canis*
Spiny dogfish	*Squalus acanthias*
Stingrays	Family Dasyatidae
Soupfin shark	*Galeorhinus zyopterus*
Tiger shark	*Galeocerdo cuvieri*
Whale shark	*Rhincodon typus*
White shark	*Carcharodon carcharias*
Whitetip shark	*Pterolamiops longimanus*
Zambezi shark	*Carcharhinus leucas*

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Influence of the hurricane on the structure of the thermocline

Parts I and III

by

Robert E. Stevenson

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Publication No. 1, 1967

INFLUENCE OF THE HURRICANE ON THE STRUCTURE OF THE THERMOCLINE [1] [2]

PART I

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Hurricane Carla entered the Gulf of Mexico through the Yucatán Straits on September 7, 1961. From there it traveled northwesterly and grew to be one of the five severest hurricanes to invade the Gulf since 1837. By September 10, as it approached the Texas coast (Figure I-1), pressures in the center were 931.2 mb, and winds of 130 knots whirled around the eye. Because of the early and continuous advisories issued by the U. S. Weather Bureau, nearly 500,000 people evacuated the coastal regions. Thus, despite the fury of the storm and the accompanying storm surges (a maximum of 7 meters where the storm crossed the coast), few persons were injured.

The energy exchange between the sea and the atmosphere is several orders of magnitude greater during a hurricane than in less severe tropical cyclones. Hurricanes provide, therefore, a unique 'laboratory' for investigations of air-sea interaction. The taking of in situ measurements of water temperature changes during hurricanes is, however, almost impossible. No work can be done aboard ship. Weather buoys have broken from their moorings, never again to be seen, and towers have foundered. Thus, changes in the water temperature distribution affected by Hurricane Carla were investigated by necessity, after the passage of the storm, when the waters were peaceful again.

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[1] Contribution No. 239, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

[2] This article is a modification of a paper by Stevenson & Armstrong (1965).

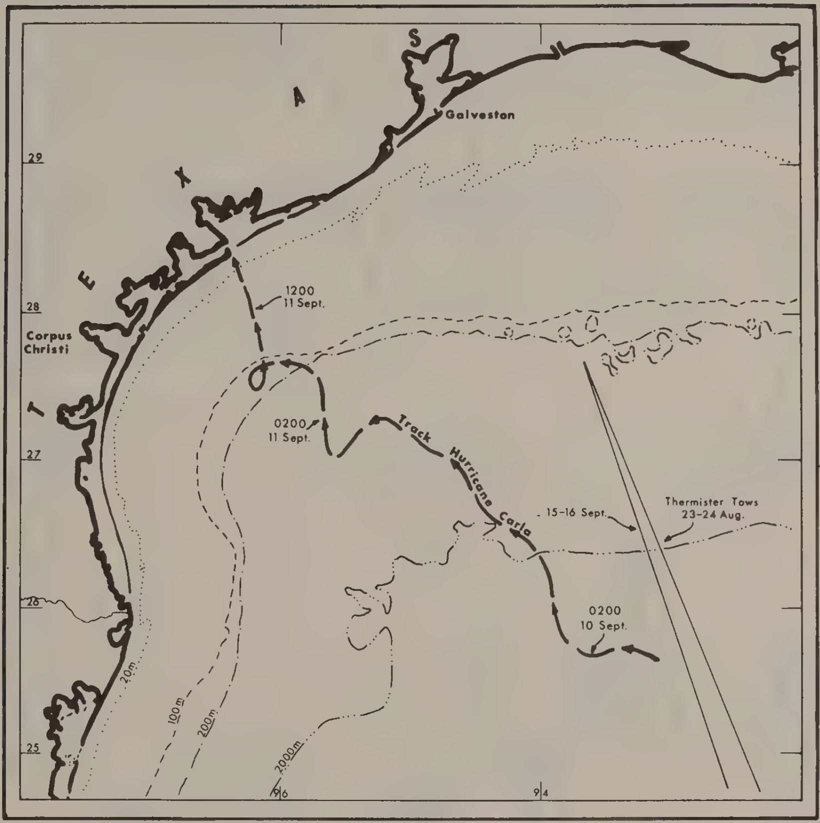

T E X A S
Galveston
29
28
Corpus Christi
27
26
25
1200 11 Sept.
0200 11 Sept.
Track Hurricane Carla
15-16 Sept.
Thermister Tows 23-24 Aug.
0200 10 Sept.
20m
100m
200m
2000m
96
94

Figure I-1.--The track of Hurricane Carla on September 10 and 11, 1961, as plotted by U. S. Weather Bureau Radar at Corpus Christi and Galveston, Texas, and locations of thermistor-chain tows made from the R/V HIDALGO.

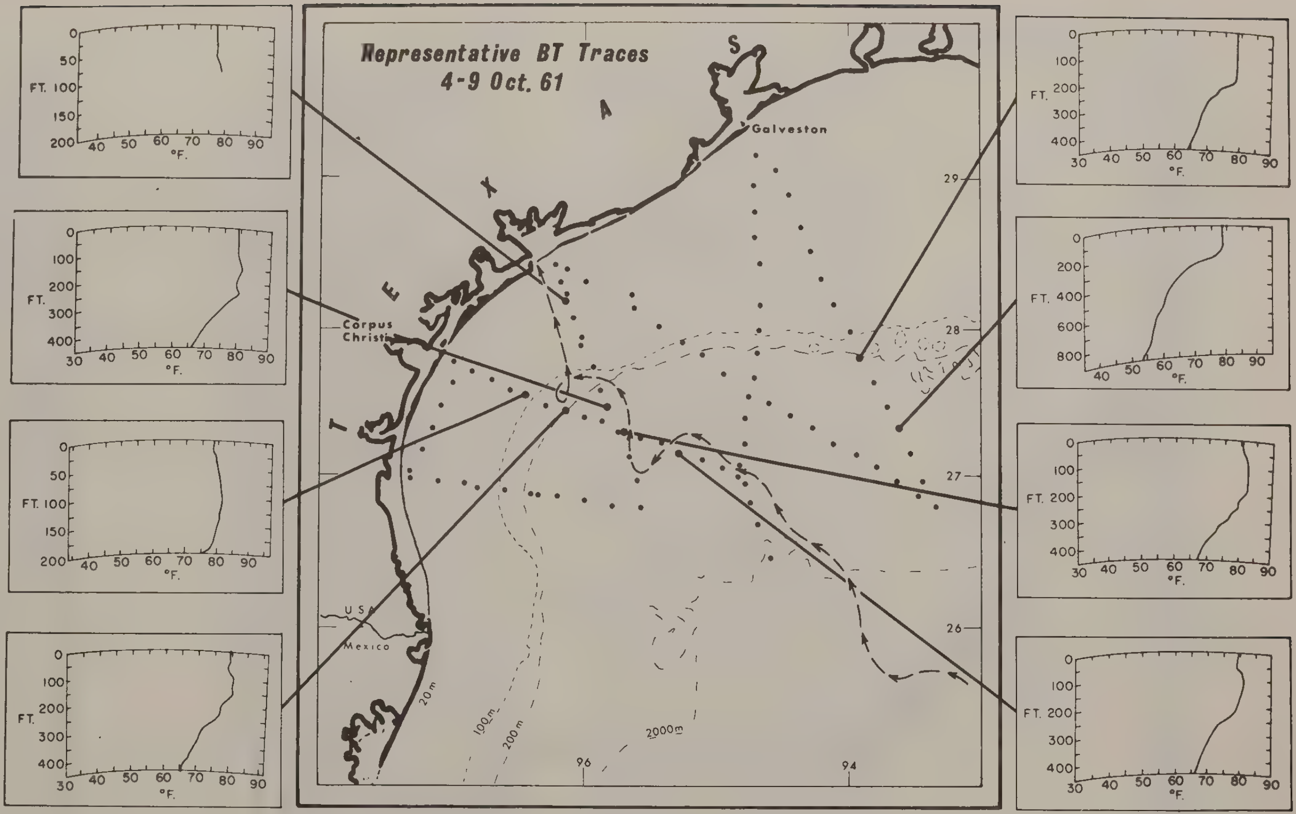

Representative BT Traces
4-9 Oct. 61
TEXAS
Galveston
Corpus Christi
U.S.A.
Mexico
29
28
27
26
96
94
20 m
100 m
200 m
2000 m
FT.
°F.
0
50
100
150
200
300
400
600
800
30
40
50
60
70
80
90

Figure I-2.--Location of bathythermograph casts made from the R/V HIDALGO on October 4-9, 1961, and representative temperature traces.

Northwest Gulf Waters in the Fall of 1961

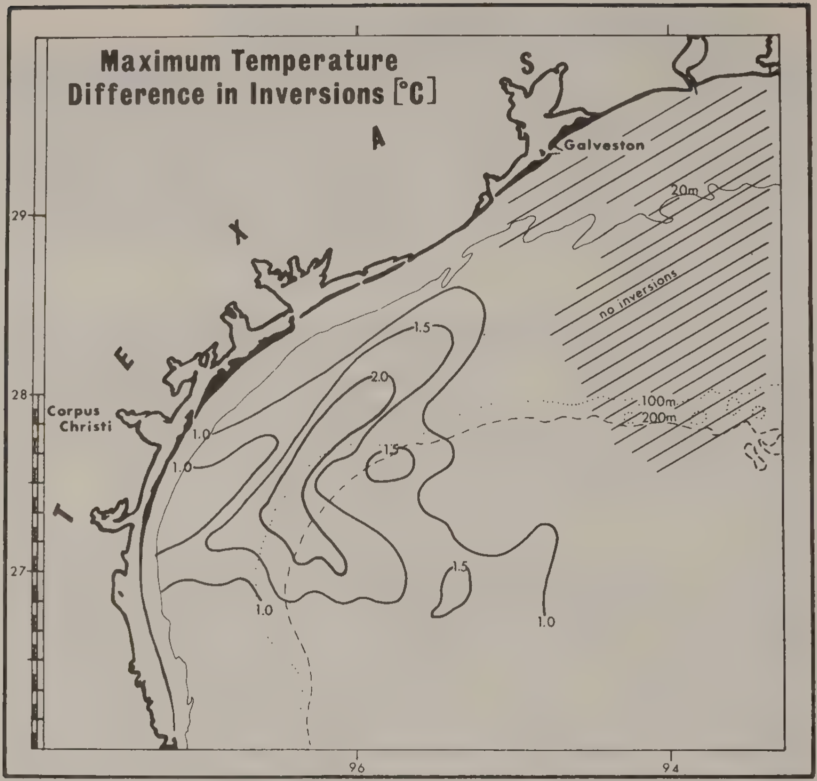
Throughout the year a layer of low-salinity water lies along the coast of the northwest Gulf. Variations in the salinity, width, and thickness of the layer depend primarily on the volume of river runoff coming through the numerous estuaries and lagoons (Harrington, 1966). Usually the surface salinity is approximately 30.00% close to shore, and this salinity may extend to depths of 20 to 30 meters; at 40 to 50 meters the salinity increases to 36.00%. A salinity of 36.50% is normal at distances of 30 to 50 km from the coast.

Rainfall along the Texas Coast was considerably greater than mean conditions during the summer of 1961 (Weather-Bureau-Galveston). It is clear then that the brackish surface water extended farther from shore than usual -- probably about 120 km from the coast between the Mexican border and Galveston, Texas. It was over this wide brackish layer that Hurricane Carla swept on September 10 and 11 (Figure I-1).

The R/V HIDALGO, Texas A&M University, cruised in the northwest Gulf, October 4-9. Scientists aboard were investigating the distribution of temperature and salinity. Many bathythermograms revealed temperature inversions as great as 2.5°C, extending to depths of 83 meters (Figure I-2). The inversions were all within the area of the brackish bulge (Figure I-3). Salinities near shore were as low as 29.76% at the surface and were 30.00 to 31.00% to depths of 40 meters. In most of this area, water of 36.00% lay below 100 meters, although at 70 to 80 meters the salinities were usually near 35.00% (Figure I-4a and 4b). Waters with the steepest salinity gradient were within 110 km of the shore, and surface waters having salinities of 33.00%, or less, extended to 210 km from shore (Figure I-4a). The typically steep salinity gradients are noted in Figure I-4b.

Apparently the loss of heat in the surface waters to the hurricane atmosphere lowered the water temperature, forming the inversions, and, because of the brackish layer, the lowered temperatures did not result in a density instability in the water. From climatologic records and previous data collected during research cruises over the outer shelf of the northwest Gulf, it is known that normal changes in water temperatures in September and October are negligible. This relation has been substantiated by applying the techniques presented by Laevastu (1960) to the factors that influence heating and cooling of surface waters. Furthermore, the 91 bathythermograms taken on the October 4-9 cruise showed no indication of heating, or further cooling, of the surface waters in the month after Hurricane Carla.

In the weeks after Hurricane Carla, winds over the northwest Gulf blew at low velocities, and several successive days



Maximum Temperature Difference in Inversions [°C]
T
E
X
A
S
Galveston
Corpus Christi
20m
no inversions
100m
200m
1.5
2.0
1.0
1.0
1.5
1.0
1.5
1.0
29
28
27
96
94

Figure I-3.--The distribution of maximum temperature differences in inversions as deduced from data gathered on October 4-9, 1961.

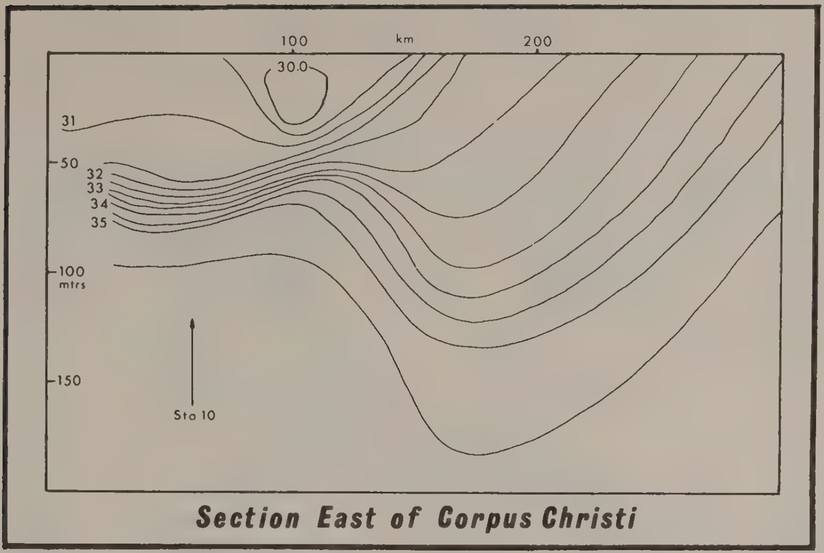


Figure I-4a.--Salinity Profile extending east of Corpus Christi, Texas. The samples were collected on October 7 and 8, 1961.

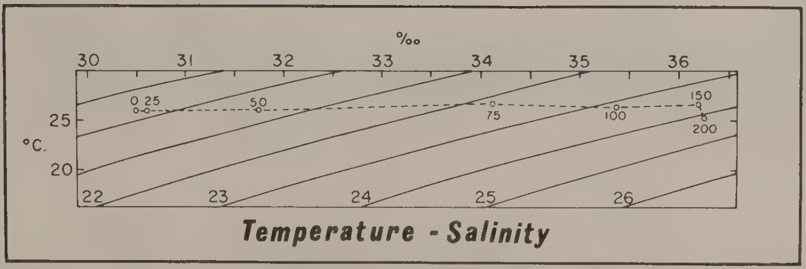


Figure I-4b.--Temperature-Salinity diagram at HIDALGO Station 10 (see Figure 4a) on October 7, 1961.

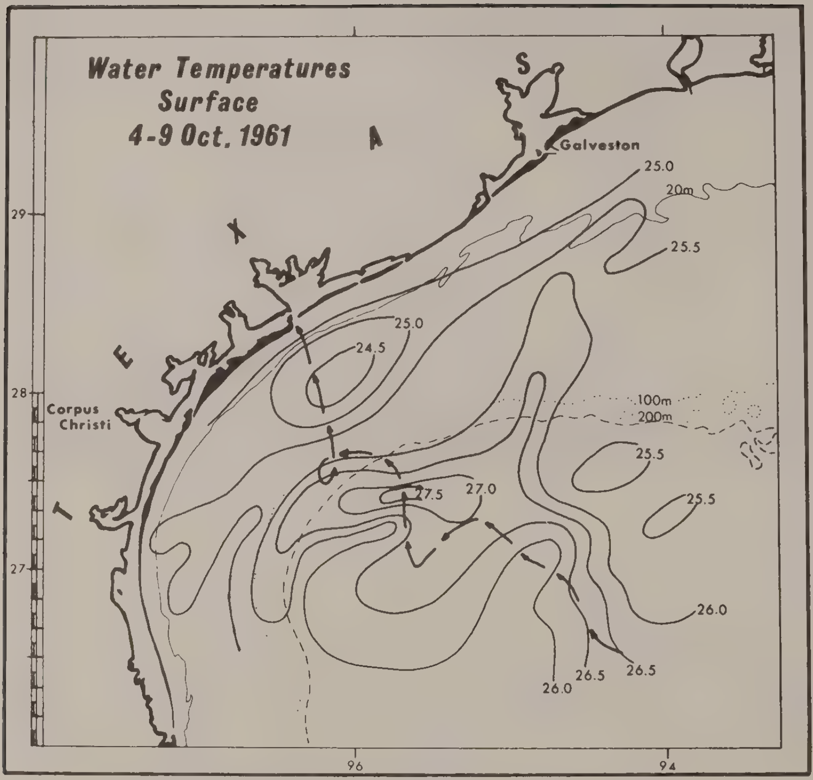

Water Temperatures
Surface
4-9 Oct. 1961
T E X A S
Galveston
Corpus Christi
29
28
27
96
94
25.0
20m
25.5
25.0
24.5
100m
200m
25.5
27.5
27.0
25.5
26.0
26.5
26.5
26.0

Figure I-5.--The distribution of surface water temperatures on October 4-9, 1961.

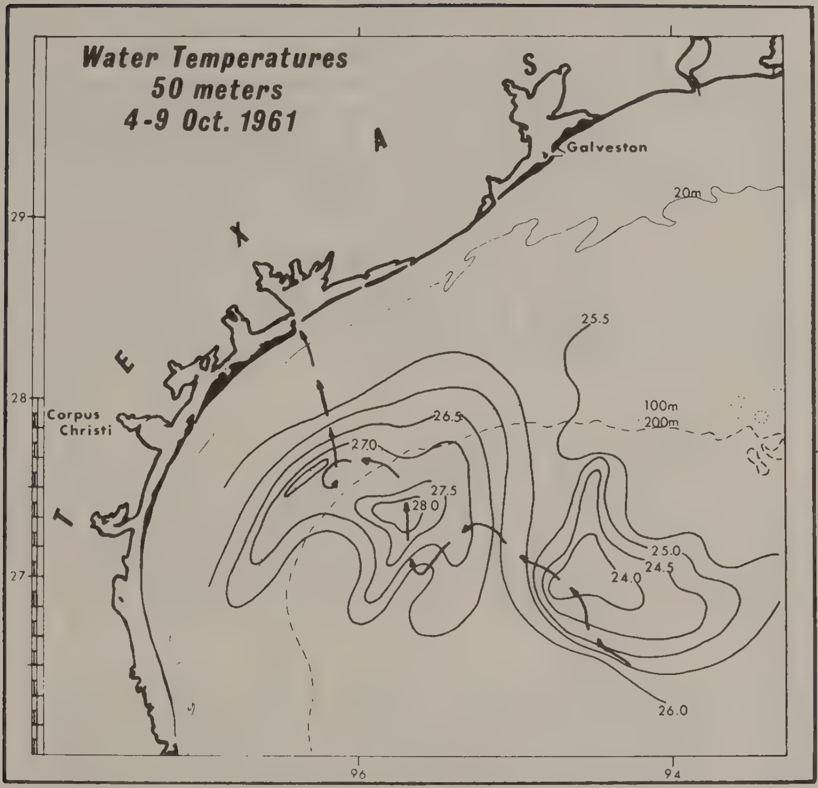

Water Temperatures
50 meters
4-9 Oct. 1961
T E X A S
Galveston
Corpus Christi
20m
100m
200m
25.5
26.5
27.0
27.5
28.0
25.0
24.5
24.0
26.0
29
28
27
96
94

Figure I-6.--The distribution of water temperatures at a depth of 50 meters on October 4-9, 1961.

had light and variable air. The wind was, as normal, from the southeast but was not strong enough to produce wind-drift currents that would re-establish normal temperature distribution. Isosteric surfaces, computed from data gathered on October 4-9, were essentially flat. Therefore, no significant density currents were present.

On the basis of these considerations it was concluded that the water-temperature structure of the northwest Gulf retained, for at least the succeeding 4 weeks, the dominant characteristics formed during Hurricane Carla. The inversions which were measured during October 4-9 were believed little modified from the configuration immediately after the hurricane.

To the southeast of Galveston, where the vertical distribution of salinity was nearly isohaline, the heat loss from the surface caused instability in the upper layers. The consequent convective stirring produced an isothermal layer which extended to depths of 60 meters (Figure I-2).

Temperature Distribution

The distribution of surface water temperatures in early October reflected the influence of Carla (Figure I-5). Warmer water was centered in the area where the hurricane deviated from its northwesterly course, whereas colder water was on both sides of the hurricane track and over that part of the shallow shelf which was beneath the track of the storm.

At depths of 50 meters (Figure I-6), the main 'cells' of warm and cold water were even more sharply defined. The effects of the temperature inversions were noted where temperatures were slightly greater than 28. 0°C, which was just more than 0. 5°C warmer than those at the immediately overlying surface. Farther from shore and to the right of the hurricane track, the cooler water indicated modified temperature structures where typical Gulf-water salinities occurred.

The influence of the hurricane was not restricted to the surface layers, for there was an upward transport of heat from depths greater than 100 meters. This movement was best exemplified by changes which took place in the vertical and horizontal configuration of the thermocline. For Figures I-7 and 8, semidiagrammatic sketches were drawn from data gathered by thermistor-chain tows along the tracks indicated in Figure I-1. (Figures I-7 and 8 were drawn from average values of the data obtained by the thermistor-chain. The temperatures and the depths of the isotherms differ to some extent, therefore, from those plotted directly from the bathythermograms.) On August 23 the thermocline was typical of these Gulf waters, exhibiting a flat

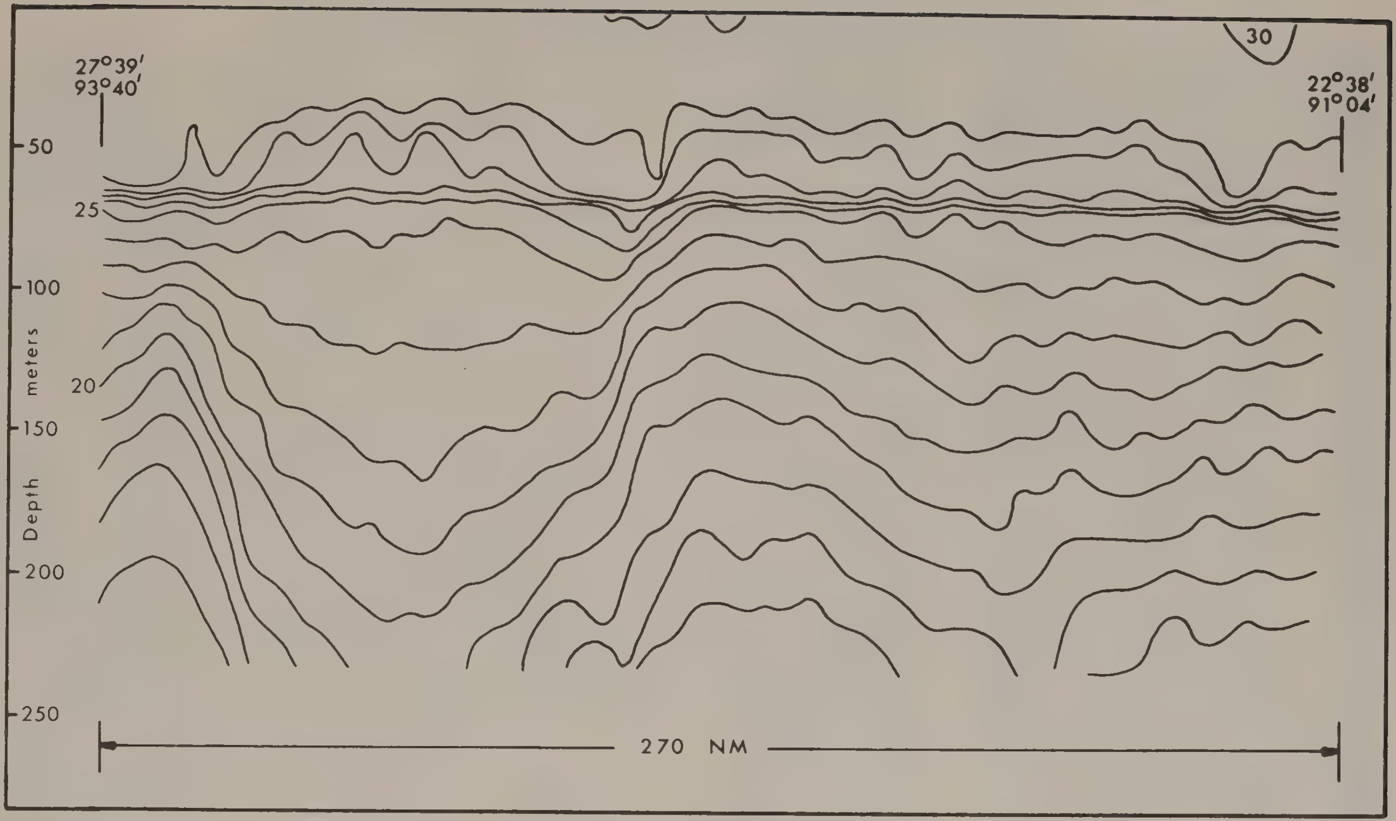


Figure I-7.--A semidiagrammatic representation of the vertical water temperature distribution south of Galveston on August 23, 1961. Data were obtained from a thermistor-chain tow made from the R/V HIDALGO.

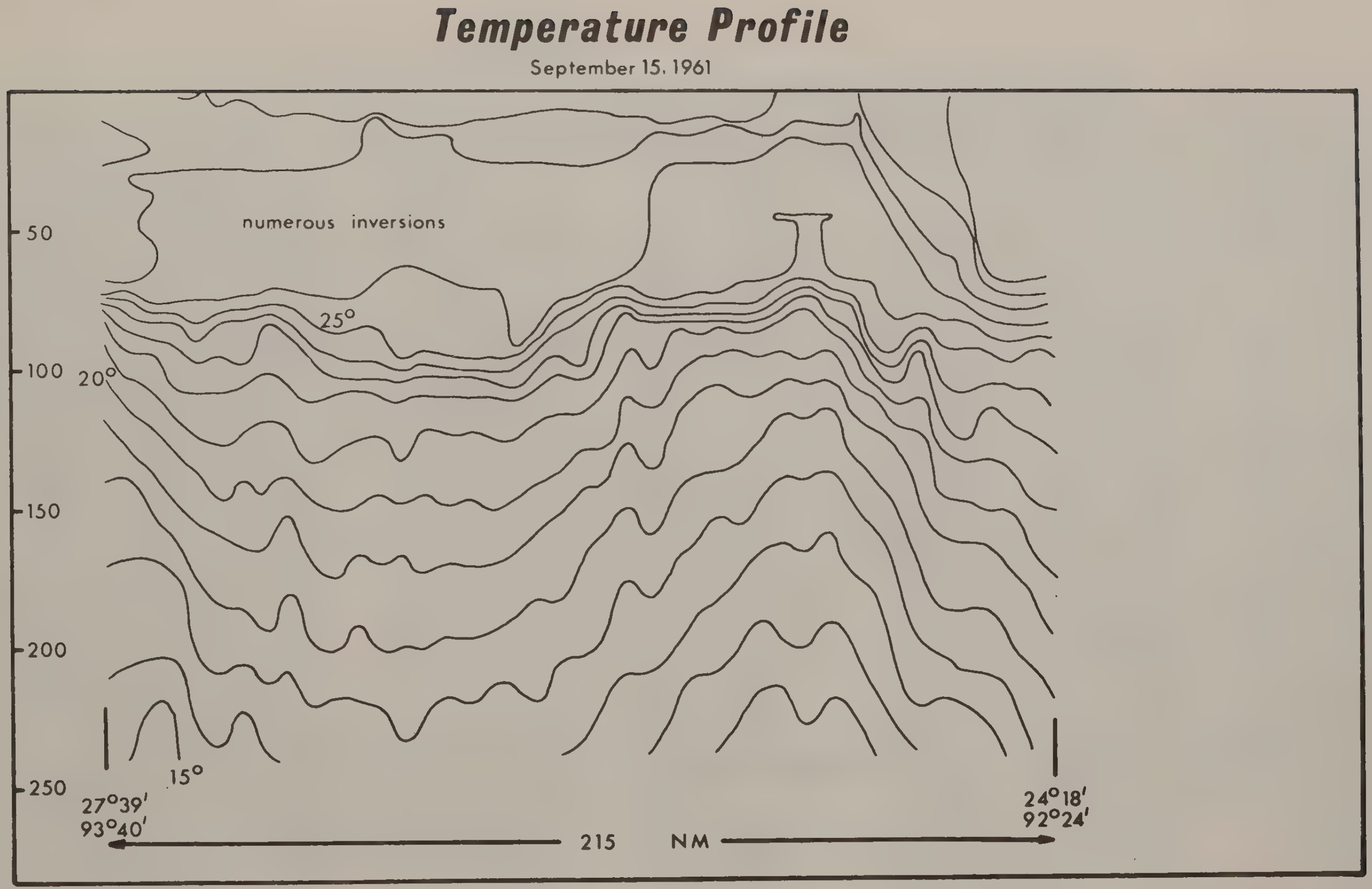


Figure I-8.--A semidiagrammatic representation of the vertical water temperature distribution south of Galveston on September 15, 1961. Data were obtained from a thermistor-chain tow made from the R/V HIDALGO.

surface at depths of 65 to 70 meters. The thickness of the thermocline decreased in an offshore direction, but the 26°C isotherm remained as the upper limit throughout the area measured.

During the hurricane, 26°C water was carried into the disturbed surface layer, and the 25°C isotherm marked the upper part of the thermocline on September 15 (Figure I-8). The surface of the thermocline was no longer flat, but had been depressed shoreward and seaward of the region where the tracks of the hurricane and thermistor tow crossed. A comparison of the two profiles (Figures I-7 and 8) reveals that after the storm the 24° and 25°C isotherms were deeper in the nearshore area and that those below the thermocline were 18 to 70 meters shallower than on August 25. The greater upward displacement was in the deeper water (note the 20°C isotherm, for example).

The topography of the 25°C isotherm (top of the thermocline) during October 4-9 closely resembled the configuration of the temperature distribution. Whereas the thermoclinal surface was generally between 50 and 70 meters south of Galveston and seaward of the shelf break, it was depressed to depths of 102 meters to the west (Figure I-8). The thermocline decreased abruptly in depth from the edge of the shelf shoreward, and, along the track of the hurricane, was absent in waters shoaler than 50 meters (see Figure I-2).

Summary

The cruises of the R/V HIDALGO in 1961 were certainly "cruises of opportunity," for the extent and magnitude of changes in the waters after a hurricane passage were unknown. Nevertheless, the temperature profile obtained on September 15, 1961 (Figure I-8), is quite similar to those from data gathered in 1964. The "stovepipe" effect beneath the "eye position" is easily noted, as is the depression of the thermocline on either side. It would appear that Leipper's analysis (1966) is correct -- that the warmer surface water was transported from the areas of the eye to lie in a "trough" along the borders of the "eye track," and that the removal of the surface water beneath the eye developed a divergence which produced the upwelling of deeper and cooler water.

The isotherms below the thermocline were at lesser depths after Hurricane Carla than before (compare Figures I-7 and 8), at least to the depths measured (about 230 meters). The configuration, however, of the isotherms below 100 meters (perhaps even 75 meters) on September 15, was nearly identical to that existing before the hurricane. This close similarity existed because Hurricane Carla crossed the southern border of a western-Gulf eddy, which formed the configuration of the isotherms below the thermocline before the hurricane. Clearly this isotherm configuration was not altered as the result of any reaction to the storm, but the isotherm depth did change.

One initial problem was to determine the origin of the deep temperature inversions. It is unlikely that the temperature inversions which were measured can have resulted from any mechanism other than cooling. Upwelling does not produce such vertical temperature distributions. An introduction of cool, low-salinity water, on the other hand, could produce inversions similar to those observed. The source of low-salinity water, however, is the estuarine system of the Texas coast which, during late summer, contains warm water (temperatures of 28°-32°C). Furthermore, and as discussed by Leipper (see part II), the wind field around hurricanes develops a wind drift (storm surges) and the water is driven into, rather than out of, the lagoons and estuaries.

Considering, then, that the inversions represent a certain amount of heat loss from the water, the magnitude and depth of the inversions would be controlled by (1) the thickness and salinity of the surface layer, (2) the intensity of the storm and the consequent reaction of the water, or (3) both.

If the water temperature is decreased sufficiently in any water to produce instability, convective stirring must take place (in addition to mechanical stirring by wave action). This stirring would eliminate inversions and a thoroughly mixed layer would be formed (as in the waters southeast of Galveston). If cooling were insufficient to cause convective stirring in the brackish surface water, but extended below the low-salinity layer, a mixed zone below the inversions would be expected. None was noted (see Figure I-2).

The salinity of the surface waters would control the magnitude of the temperature inversions. If cooling were to bring the water to a density instability, convective mixing would result. Conceivably, then, the loss of heat could have produced greater temperature differences than observed in the inversions.

The temperature-salinity curve in Figure I-4b shows that the water to 150 meters (at this station) was far less stable than normally encountered, but still did not reach a neutral stability (a frequent condition in the Gulf during the winter). The temperature decrease was not, therefore, the maximum possible without overturning under the prevailing water conditions. Thus, the observed temperature differences in the inversions are considered minimum.

Upwelling and Cooling

The discussion by Leipper (see Part II) of the water temperatures after Hurricane Hilda impressively described the mass transport of surface water from the region underlying the eye. Such a picture is not obvious from the data obtained after Hurricane Carla. Rather, the temperature inversions are ascribed to cooling of the water.

Certainly, if there were upwelling in addition to the heat loss indicated by the inversions measured in 1961, it is clear that the cooling extended to an even greater depth than indicated by the temperature curves. With the data we have, any estimation of how much greater would be pure folly. Nonetheless, it now seems apparent that the heat loss from the water must have been orders of magnitude more than the 2.2×10^{18} cal/24 hours originally calculated (Stevenson & Armstrong, 1965).

Acknowledgements

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PART III [1]

Robert E. Stevenson, Research Oceanographer
Bureau of Commercial Fisheries
Galveston, Texas

I think you can begin to understand that our investigations of hurricanes have been somewhat fortuitous. It almost seems that we spend the summer hoping that if one does come, a ship will be available.

Dale Leipper has mentioned some of the deep-water temperature structures before and after Hurricane Betsy. Of interest to fishery oceanographers is the effect of hurricanes in the shallow water -- particularly in the Gulf where the great shrimp fishery is located. I shall discuss now the modification of the water temperatures over the Gulf shelf by Hurricane Betsy.

Hurricane Betsy entered the Gulf of Mexico on September 8, 1965, after crossing the southern tip of Florida. The storm followed a northwesterly path and penetrated the coast west of New Orleans, Louisiana, in the late hours of September 9. Hurricane-velocity winds extended 130 kilometers from the center and wind speeds of 190 km/hr were measured near the eye. The average forward speed of the storm as it crossed the Gulf of Mexico was 24 km/hr.

The complete track of Hurricane Betsy, from the time it was first noted as a tropical depression off the northeast coast of South America, through its period as a tropical storm northeast of Haiti, and its life as a hurricane are shown in Figure III-1. During early life, as a tropical depression, Betsy was photographed by Col. Gordon Cooper and Cdr. Charles Conrad as they orbited on GT-5 (Figure III-2) near the mouth of the Orinoco River, Guyana (British Guiana). The astronauts did not know that this was a tropical depression; that this was Hurricane Betsy at its birth, for they could have centered it in the photograph.

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[1] Contribution No. 239, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

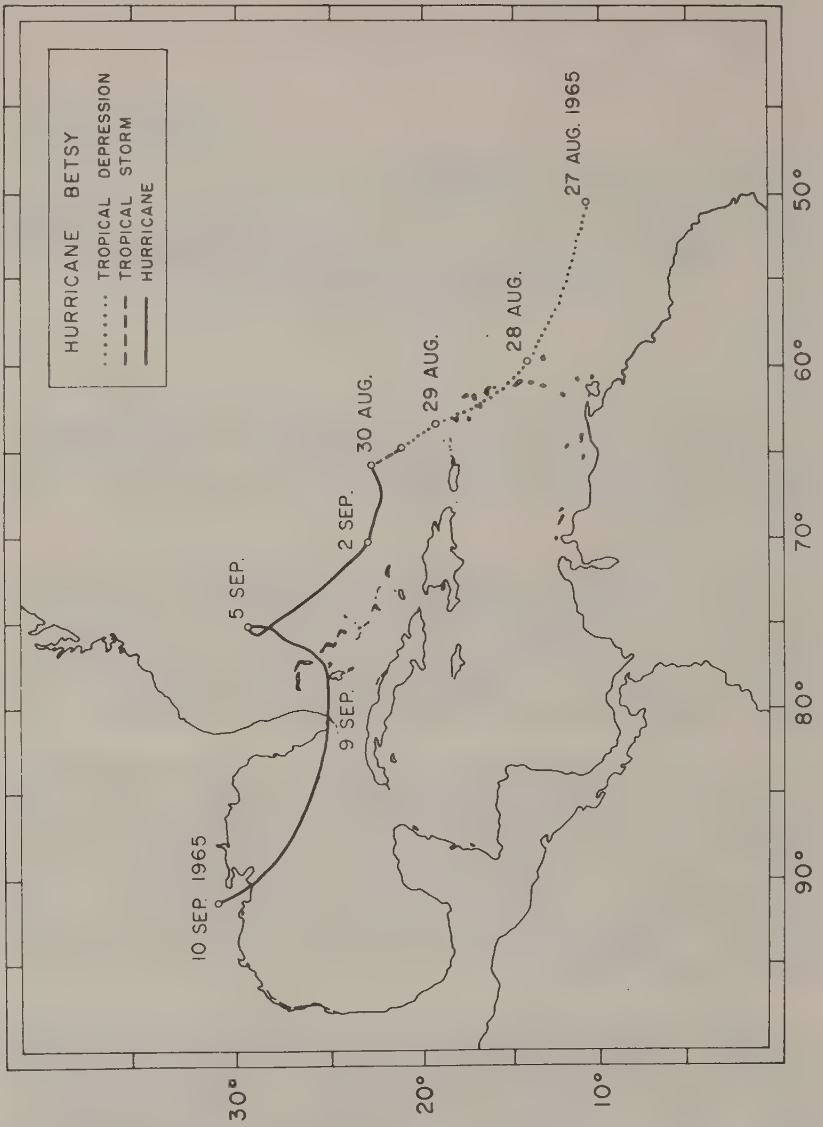
HURRICANE BETSY
TROPICAL DEPRESSION
TROPICAL STORM
HURRICANE
27 AUG. 1965
28 AUG.
29 AUG.
30 AUG.
2 SEP.
5 SEP.
9 SEP.
10 SEP. 1965
50°
60°
70°
80°
90°
30°
20°
10°

Figure III-1.--Track of Hurricane Betsy, including those areas over which the storm traveled during its period of a tropical depression and a tropical storm.

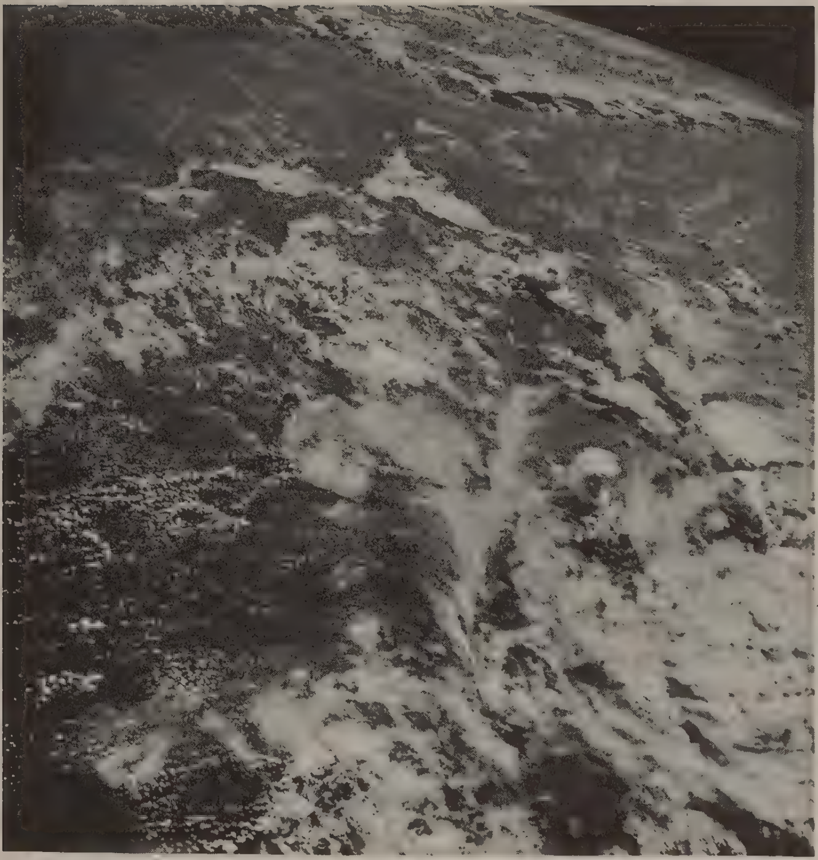

Figure III-2.--Photograph of the area off the coast of British Guiana showing embryonic Hurricane Betsy in foreground. Photograph was taken on Gemini V by pilots Lt. Col. L.G. Cooper and Cdr. Charles Conrad, Jr.

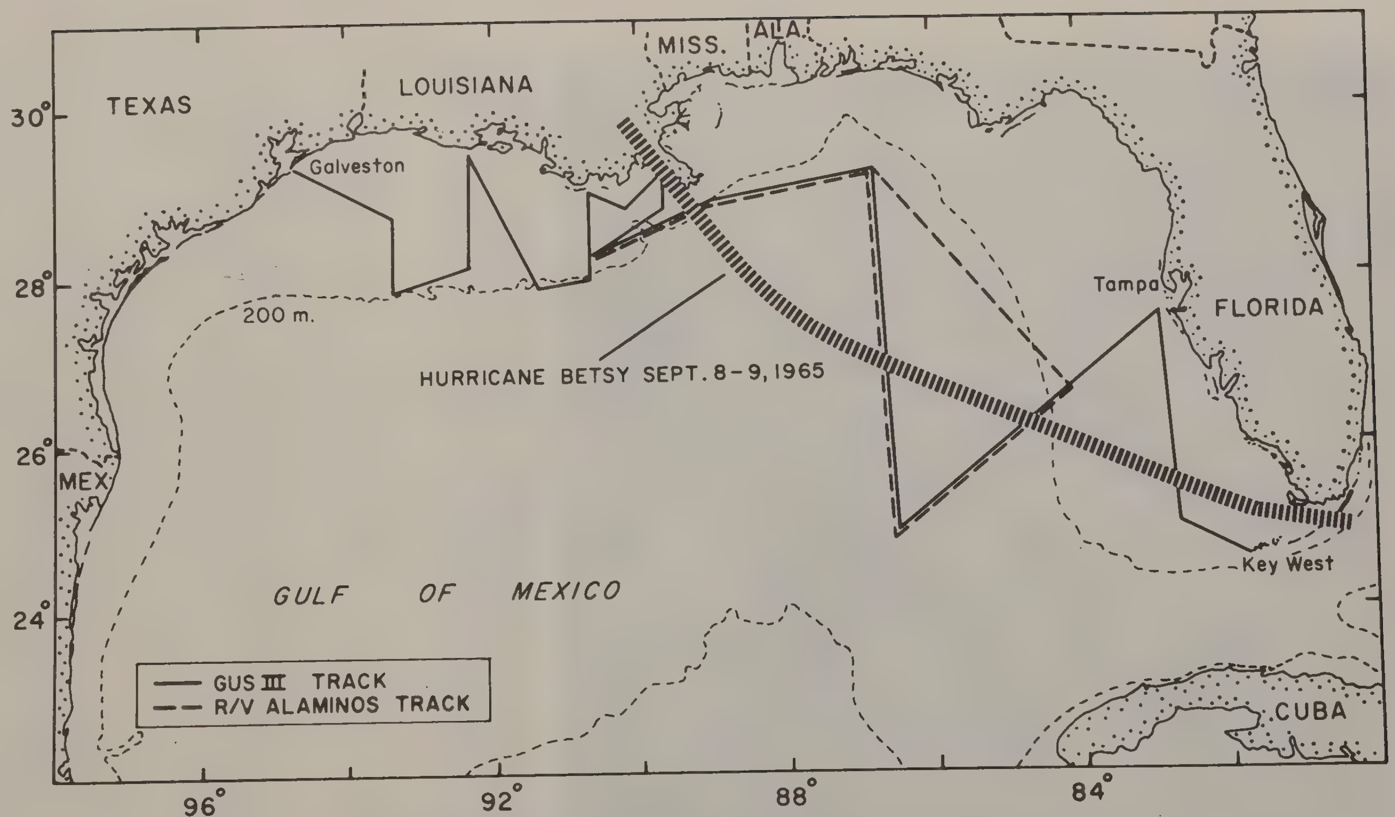
MISS.
ALA.
LOUISIANA
TEXAS
30°
Galveston
28°
200 m.
HURRICANE BETSY SEPT. 8-9, 1965
Tampa
FLORIDA
26°
MEX
Key West
24°
GULF OF MEXICO
GUS III TRACK
R/V ALAMINOS TRACK
CUBA
96°
92°
88°
84°

Figure III-3.--Part of the tracks of oceanographic stations occupied by the R/V ALAMINOS and complete track of the M/V GUS III in August and September, 1965.

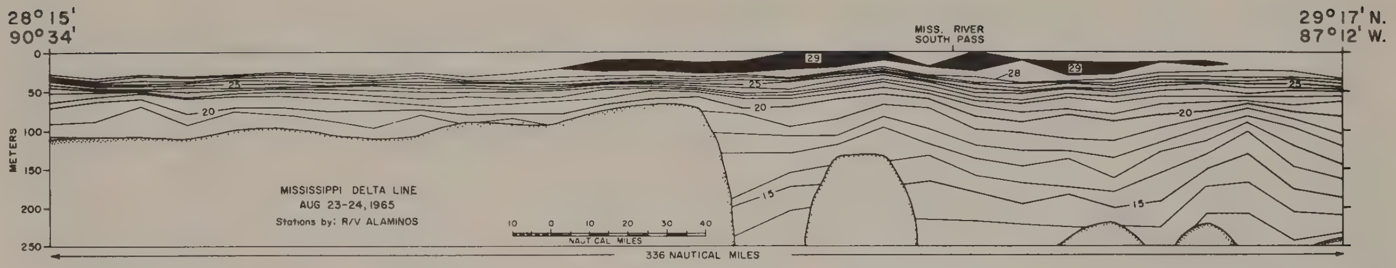

Figure III-4a.--Temperature profile in the waters off the Mississippi Delta, from data gathered aboard the R/V ALAMINOS, August 23-24, 1965. Warm Mississippi River water, with temperature inversions of 1-2.5° C, is shown in black.

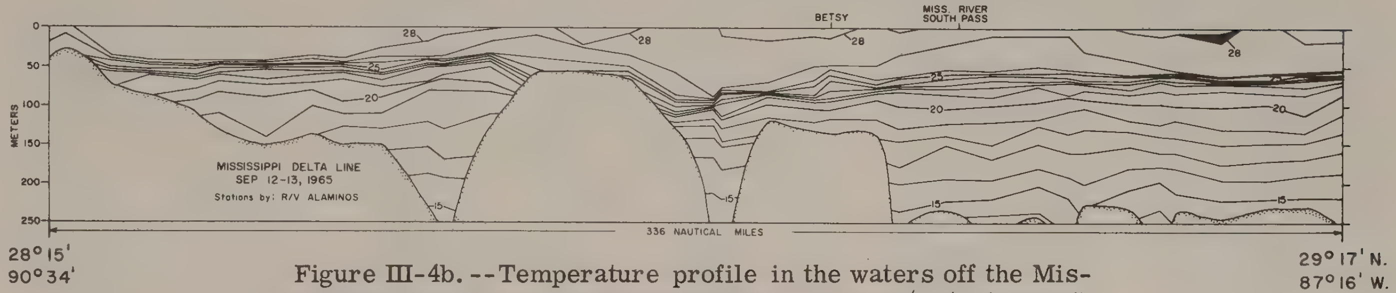

Figure III-4b.--Temperature profile in the waters off the Mississippi Delta, from data gathered aboard the R/V ALAMINOS, September 12-13, 1965. Note: The only occurrence of water with temperature inversions is to the east of the Delta.

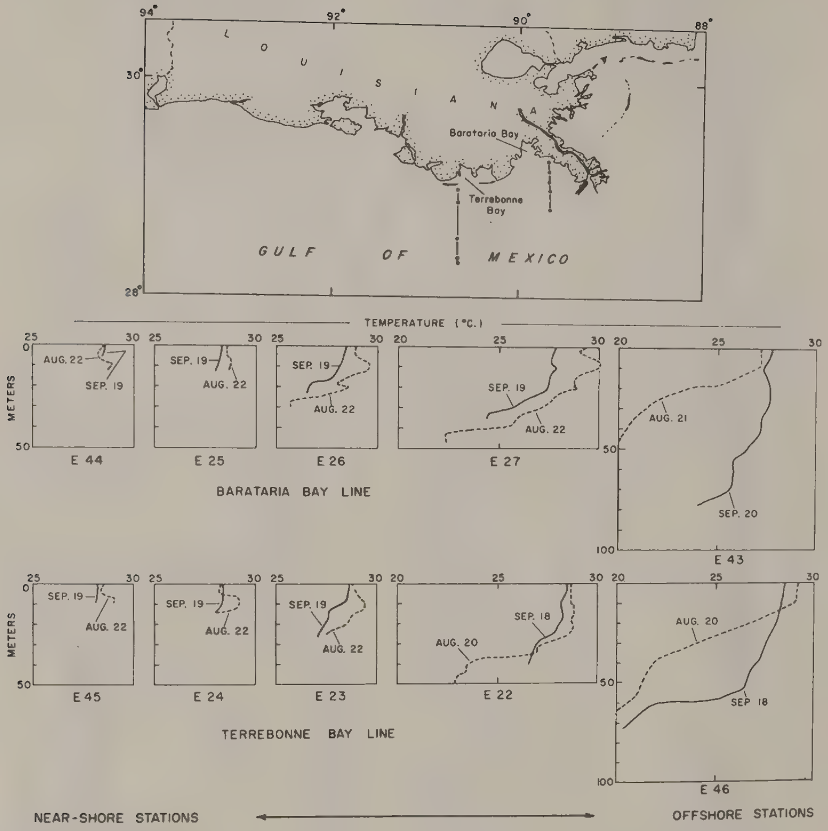

Figure III-5.--Reconstruction of temperature traces from bathythermograph casts made from the M/V GUS III in August and September, 1965.

The R/V ALAMINOS, Texas A&M University, with Dr. Leipper as chief scientist, cruised along the edge of the continental shelf and occupied a series of oceanographic stations on August 23-24, 1965. Immediately after the storm, on September 12-13, the ALAMINOS cruised again along the same track. Ten days later, September 20-22, the M/V GUS III, Bureau of Commercial Fisheries, occupied stations along one of the tracks made earlier by the ALAMINOS (Figure III-3). The data collected on these cruises allowed, for the first time, analyses of the water structure immediately before and after the hurricane.

In August, the water near the Mississippi Delta had a warm surface layer spread over water of normal temperature (Figure III-4a). The top of the thermocline was bounded by the 28°C and 29°C isotherms and began at depths of 20 to 30 meters. The thermocline was nearly horizontal, in an east-west direction, and the net water motion was parallel to the coast. (The GUS III encountered westerly flowing currents of 3-5 knots on September 20-21.) Hurricane Betsy crossed these waters about 25 nautical miles west of South Pass.

The temperature structure shortly after the passing of Hurricane Betsy was considerably different from that which prevailed in August (Figure III-4b). The thermocline was deeper in all areas than it was in August -- the depth of the top varied from 40 to 90 meters. The greatest depths of the thermocline were in the water which lay under the eye of the storm.

As Dr. Leipper has mentioned, the Ekman transport of water is away from the eye of a hurricane. Water is pushed ahead of the hurricane, therefore. As it reaches the coast, a storm surge occurs and, at the same time, the warm surface water forms a deepening wedge along the coast (Leipper, 1966). This effect can be noted in the Mississippi Delta profile (Figure III-4b) where water of 25°C lies atop the shelf after the hurricane, whereas 19°C water covered the shelf in August (Figure III-4a). The dramatic change in the temperature structure off Barataria and Terrebonne Bays before and after the hurricane (Figure III-5) attests to the hurricane influence. Note especially Station E-43 off Barataria Bay (over which the hurricane passed) and E-46 off Terrebonne Bay. The change in the structure of the thermocline off Terrebonne and Barataria Bays indicates that the intrusion of offshore water was extensive and produced significant changes in the temperature structure.

The isotherm marking the top of the thermocline after the hurricane differed from the August condition; it was cooler by 2°-3°C along much of the section, and differed from one place to another along a transect across the path of the hurricane (Figure III-4a and 4b; top of the thermocline was 28° -29°C in Au-

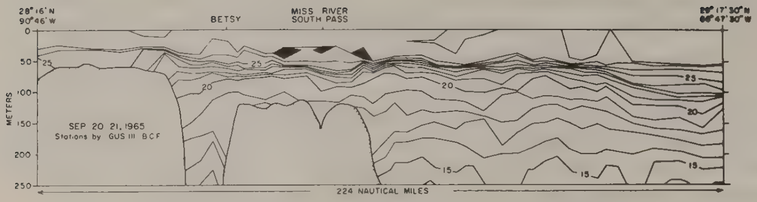

Figure III-6a.--Temperature profile in the waters off the Mississippi Delta, from data gathered aboard the M/V GUS III, September 20-21, 1965. (Blacked-in portions indicate temperature inversions.)

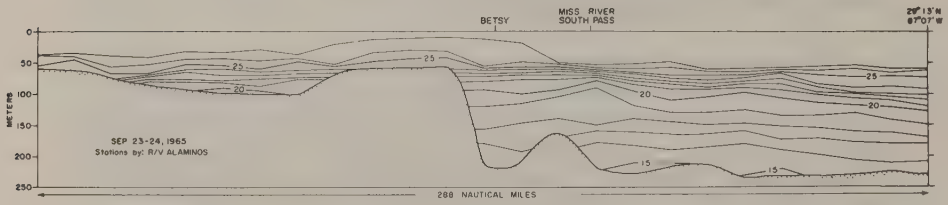

Figure III-6b.--Temperature profile in the waters off the Mississippi Delta, from data gathered aboard the M/V GUS III, September 23-24, 1965.

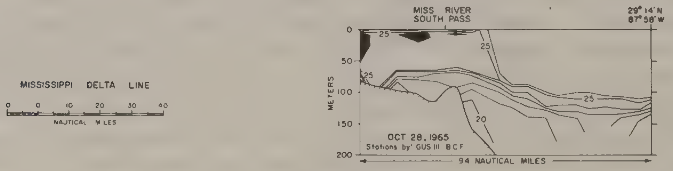

Figure III-6c.--Temperature profile in the waters off the Mississippi Delta, from data gathered aboard the M/V GUS III, October 28, 1965. (Blacked-in portions indicate temperature inversions.)

gust and 26° -28°C in September). Beneath and for about 100 nautical miles east and west of the path of the eye, the top of the thermocline was bounded by the 26°C isotherm along the Mississippi Delta Line (Figure III-4b). Beyond 100 nautical miles, the isotherm at the top of the thermocline was either 27°C or 28°C, but in all areas it was at least 1°C less than in August.

Above the thermocline, there was little indication of warm Mississippi River water along the offshore series of oceanographic stations on September 20-21. The only remnants of the extensive, pre-hurricane layer of brackish water lay east of the Delta.

Ten days after Hurricane Betsy had crossed the northern shelf of the Gulf of Mexico, the thermocline beneath and to the east of the path of the storm lay at depths between 40 and 50 meters (Figure III-6a). West of the path the top of the thermocline was between 20 and 50 meters. In all waters except those immediately beneath the path of the storm, the top of the thermocline was bounded by the 27°C isotherm. Beneath the path of the eye, 26°C continued to mark the top. Brackish water had returned to the surface layers mostly off the mouth of the Mississippi River.

Two days after the GUS III completed the line of stations off the Mississippi Delta, the ALAMINOS returned to the area (Figure III-6b). The differences in the temperature structures in the 2-to 3-day period were negligible. Those which appear to have been present, as depicted in Figures III-6a and 6b, can be disregarded because the GUS III was closer to the coast and occupied stations at shorter intervals than the R/V ALAMINOS.

The GUS III returned to the waters off the Delta about 1 month later (October 28, 1965, Figure III-6c). Although the earlier line of stations was not completed, it was clear that the effects of the hurricane were no longer present, and that changes from conditions in September were large.

Summary

It is clear that the waters over the northern shelf of the Gulf were profoundly modified by the hurricane. The typical surface waters near shore were removed and replaced by waters with oceanic characteristics. This change is best shown in the temperature profiles by the removal of warm, surface water. The influence of the hurricane extended to the greatest depths of the continental shelf (75 meters) so that water temperatures on the shelf floor were as much as 6°C warmer after the storm than before.

Upwelling in the upper 30 meters of the water column was evident at distances of about 60 nautical miles on either side of the eye of the hurricane. A 50-meter-thick layer of isothermal water lay on the surface at distances of about 100 nautical miles to either side of the path. Surface currents flowed strongly to the west in the area seaward from the Delta. Although modified to some degree, these features were still present 10 days after the storm had passed over the northern shelf.

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Reprinted from Transactions of the American Fisheries Society
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pp. 359–361

Aquarium Susceptibility of Tagged and Untagged Atlantic Herring to Predation

Estimates of fish population by tagging require a knowledge of the mortality attributable to the tags—not only of deaths caused by the tagging itself, but also of deaths caused indirectly by increasing the vulnerability of the fish to natural hazards. To evaluate the effect of tags on the susceptibility of herring (*Clupea harengus harengus* L.) to predation, groups of tagged and untagged herring were exposed to three common predators in a circular wooden tank, 2.5 m in diameter by 1 m in depth.

The herring, 10–12 cm in total length, were placed in the tank with the following predators: three shorthorn sculpin (*Myoxocephalus scorpius* L.) about 30 cm long, three cod (*Gadus morhua* L.) 30–50 cm long, and four pollock (*Pollachius virens* L.) 30–50 cm long. These species were selected because they were readily available and relatively hardy; although they undoubtedly prey on herring to some extent in nature, they are not necessarily the most important predators. The herring were tagged through the musculature anterior to the dorsal fin with the vinyl spaghetti loop described by Watson (1963). Losses from predation were noted either by making direct counts of the herring at intervals of 10 and 30 minutes after introduction or, when the numbers were large, by taking photographs from a position above the tank.

OBSERVATIONS OF PREDATION ON TAGGED AND UNTAGGED HERRING

Experiment 1. Ten tagged and 10 untagged herring were placed in the tank with the predators once each day for 12 days. The tags were bright yellow and clearly visible in the water. Although the proportions of tagged and untagged fish eaten varied each day, the 12-day totals were 41 tagged and 34 untagged eaten after 10 minutes, and 68 tagged and 63 untagged fish eaten after 30 minutes. A chi-square test indicated no significant difference between the groups.

Experiment 2. One hundred each of untagged herring and herring tagged with bright

TABLE 1.—*Numbers of Atlantic herring eaten each day by predators from an initial group of 100 untagged fish and 100 fish tagged with high-visibility yellow tags*

	Number eaten		Cumulative number eaten	
Day	Tagged	Untagged	Tagged	Untagged
1	31	31	31	31
2	35	37	66	68
3	14	8	80	76
4	5	4	85	80
5	9	15	94	95

TABLE 2.—*Comparison of the effort required to catch single tagged and untagged herring*

	Tagged	Untagged
Mean number of attempts made	4.6	5.2
Mean time required (seconds)	50.3	122.9
Mean number of attempts per second	0.22	0.16

yellow tags were placed in the tank at one time. Counts were made photographically once each day, beginning one hour after the introduction for five days. The difference in the numbers of tagged and untagged fish eaten each day or cumulatively was small (Table 1). The greatest differences in the cumulative counts were on the 3rd and 4th days, but these differences were not significant at the 5% probability level for appropriate chi-square values.

Experiment 3. Equal numbers, varying from 5 to 12 individuals in each category, of tagged and untagged herring were put in the tank with the predators each day for 9 days. The tags were similar to those used in experiments 1 and 2 except that they were transparent and nearly invisible in the water. The daily consumption of tagged herring was consistently higher during the first 10 minutes than that of the untagged herring. This margin decreased somewhat between 10 and 30 minutes. At the end of 9 days, the total number of tagged herring eaten in the first 10 minutes was 46, significantly higher than the 27 untagged herring eaten during the same period ($\chi^2 = 4.44$, $P < 0.05$). The total of 62 tagged herring eaten after 30 minutes was not, however, significantly different from the 44 untagged herring eaten in the corresponding interval ($\chi^2 = 2.72$, $P = 0.1$).

Experiment 4. Thirty-four yellow-tagged and 32 untagged herring were introduced singly and alternately into the predator tank, each introduced only after its predecessor had been eaten. The number of attempts to capture each herring and the time required to capture it were recorded. Differences between tagged and untagged herring for number of attempts, elapsed time, or number of attempts per unit time, analyzed by a t-test, were not significant (Table 2).

INFLUENCE OF TAGS ON VULNERABILITY

The presence of a tag on a small fish may affect its susceptibility to predation by attracting the attention of predators, or by interfering with the speed and maneuverability of the victim. Although no greater susceptibility of tagged herring was apparent when the tags were yellow, transparent tags seemed to make the tagged herring significantly more vulnerable than untagged ones. Since all the tags were made of the same material and were of the same size, all would seem to provide the same handicap to the herring, but could differ in effect on the predators because of differences in visibility. Yellow is probably highly visible to fish; in the few fish upon which studies have been made, the color sensitivity peak seems to lie in the yellow-through-blue portion of the spectrum.

The sculpin and certain gadoids have a broad range of color sensitivity (Nikolsky, 1960), including yellow; consequently the predators used in the present experiments could in all likelihood see the yellow tags very clearly. The transparent tags, which had no color and had an index of refraction near that of water, were very poorly visible to the human eye and probably to the predators. The question then is, why should the predators show little selectivity on fish with tags which they can see readily, but show significant selectivity for fish with tags which they can see poorly, if at all? If the tags acted both as an attraction to the predators and an impediment to the herring, one would expect significantly greater predation on the herring marked with yellow tags. If the tags had no effect on the predators, but were solely an impediment to the herring, no difference should appear between the experiments with yellow tags and those with transparent tags.

The simplest explanation consistent with the results is that the yellow tags had a repellant effect on the predators, as was sometimes indicated by their behavior. Several times pollock or cod when attacking a herring with a yellow tag changed their intentions and swerved aside. On another occasion, a sculpin headed for a group of three herring changed course to select the one untagged individual from the group.

If the yellow tags had a deterrent effect on the predators, why were not significantly fewer yellow-tagged herring captured by the predators? The simplest answer seems to be that the deterrent effect on the predator and the impediment of the tag to the herring, tending to produce opposite results compensated one another—the yellow tag made the herring less likely to be attacked, but also less able to escape when it was attacked. The vulnerability of yellow-tagged herring in the sea would depend on the extent to which this balance was maintained in a natural, open environment.

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Physiology of Marine Organisms and Adaptation to their Environment

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A simple laboratory technique for showing the effect of salinity on organisms is discussed in this article; biology teachers will want to try many variations.

Introduction

The distribution and seasonal occurrence of marine organisms are determined to a large extent by the relation between the physiological characteristics of the organisms and the properties of their environment. Although the sea is rather uniform as compared with the terrestrial environment, important seasonal and geographic variations do occur. Some of the environmental variables which play significant roles in the lives of the living creatures of the sea are temperature, salinity, light, tides, and currents. The mechanisms through which these factors operate are varied and often complex. The purpose of this section is to study one of the better understood of these mechanisms as an example of the kind of relations that are involved.

The organisms which inhabit the bays and estuaries of the coastal regions are often subjected to strong changes of salinity, and sometimes to very dilute or brackish seawater. Many of these organisms are well adapted to such changes and are able to endure them with no ill effects. Such organisms, called "euryhaline" species, may possess different physiological mechanisms to become so adapted, however. The chief difficulty is that of dilution of the blood and other body fluids by osmosis, since normally their blood has a salt concentration similar to that of full-strength seawater. In diluted seawater, external water tends to permeate the tissues and dilute the blood.

One way to cope with this problem is to eliminate the excess water as fast as it enters. Removal of water is accomplished by a kidney or kidney-like organ, but can only be done against the osmotic gradient through the expenditure of energy (i.e., work must be done). The source of this energy is the metabolic oxidation of food reserves, and the production of energy is accompanied by an increased consumption of oxygen. As the reaction is essentially chemical, it is directly proportional to the temperature, proceeding slowly in cold water and more rapidly in warm water. It follows, then, that when the salinity is low and the water is warm, the

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animal can get rid of excess water more readily than when the water is cold. In very cold and highly diluted seawater, the elimination of water may not be fast enough to keep pace with the intake; in this situation the animal may die or be forced to migrate to saltier water. A typical example of this kind of organism is the common green crab, *Carcinides maenas*.

Another way to cope with low salinity is merely to permit the water to enter the tissues. In some organisms this water intake has no ill effects. As the water enters, the animals swell noticeably and increase in weight. Upon return to saltier water, the weight again decreases as the water leaves. An example of such an organism is a worm known as *Phascolosoma gouldii*.

Demonstration

Materials

1. Four or more small live green crabs (30 to 50 mm across the shell).
2. Four or more live *Phascolosoma* worms (They can be procured from marine biological supply houses, or can be collected in intertidal flats in many localities south of Boston, Mass.)
3. Four small aquaria.
4. Laboratory balance capable of weighing to 0.1 gram.
5. Paper towels.
6. Five to 10 gallons of seawater of 30 o/oo or more salinity.
7. Five gallons of pond water or demineralized tap water (Both water supplies should stand at room temperature several hours or overnight.)
8. Pencils, note paper, and graph paper.

Procedure

Two of the aquaria are filled with full-strength seawater and two with diluted seawater made with equal volumes of fresh and salt water. Four small crabs are carefully wiped with a towel to remove excess water from the body surface, and are then weighed to the nearest 0.1 gram. Two are placed in the container of full-strength seawater, and two in the container of diluted seawater. The two crabs in each container should be of slightly different sizes or otherwise marked for identification.

Similarly, four *Phascolosoma* are wiped to remove excess water, weighed, and placed in the other two containers. After 20 minutes, and at 20-minute intervals thereafter, each of the animals is removed, wiped, weighed, and then returned to the appropriate container. Care must be taken to ensure that the animals are suitably identified and that weights are recorded for the proper individual each time. The weights and time of removal from the water are recorded. Weighings should be continued for at least one hour. Results are better after 2 or 3 hours. If time is available, the animals in diluted seawater can be returned to full-strength seawater and the weighings continued. For additional interest, the experiments can be repeated at higher and lower temperatures.

Expected Results

The results can be presented conveniently as a graph, where time is shown on a horizontal scale, and weight on a vertical. The vertical scale should include the smallest and largest weight observed and the horizontal scale should be marked off into as many units as the number of times the animals were weighed, each unit representing 20 minutes. The weights of the different individuals can be plotted in different colors, or on separate sheets. The plotted points (weights) of each individual should be connected by lines (Fig. 1).

Compare the graph lines for green crabs with those for *Phascolosoma*. The weights of crabs should not have changed much and the line should be more or less horizontal. The weight of the worms, on the other hand, should have increased rather rapidly for the first hour, less so thereafter.

Minor variations in weight, even apparent increases, may be observed in the crabs, due to the difficulty of removing all excess external water which may become trapped in the gill chambers or around the mouth parts. The general trend, however, should show no appreciable increase in weight. It might be supposed that the shell itself would be largely responsible for preventing the undesired osmotic intake of water by the crabs. One should remember, however, that the shell does not hermetically seal all of the soft parts of the crab. The gills, located in chambers under the sides of the body shell

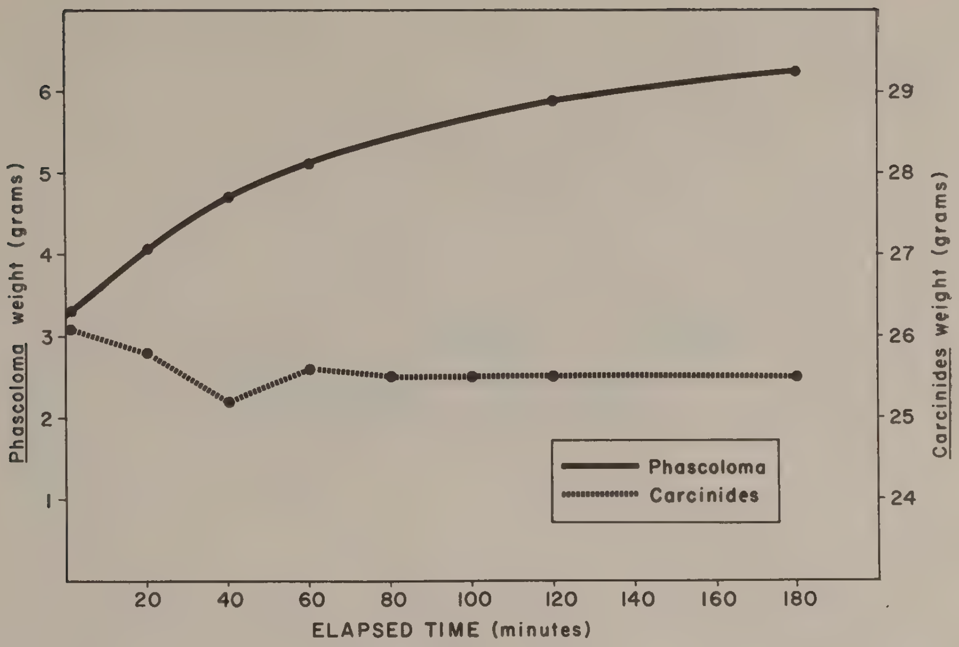

Fig. 1. Changes in weight of a worm *(Phascolosoma gouldii)* and a green crab *(Carcinides maenas)* after immersion in diluted (50%) seawater at 20° C. Although crab shows only minor fluctuations not exceeding 3% of its initial weight, the worm nearly doubles its initial weight.

just above the bases of the legs, are constantly flushed with the environmental water, passing in through the mouth parts. It is through these gills that much of the water intake occurs. Excess water, along with metabolic wastes, is removed by the "green glands" or kidneys, located in the head near the bases of the antennae.

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Observations on the Biology of the Lousefish, *Phtheirichthys lineatus* (Menzies)

Donald W. Strasburg

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Observations on the Biology of the Lousefish, *Phtheirichthys lineatus* (Menzies)

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THE LOUSEFISH, *Phtheirichthys lineatus* (Menzies), is a slender member of the Echeneidae which is often free-swimming but which also attaches to immotile objects or slow-swimming fishes. It is pantropical, uncommon, and little known biologically.

This paper reports on 24 lousefish in the collections of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu. Capture data for these specimens are presented in Table 1. Most of the other data were derived from preserved fish with the exception of one 256-mm specimen which was maintained alive in a swimming pool for several weeks.

Mr. Richard D. Samuels and Mr. Richard N. Uchida captured the fish, Mr. Everet C. Jones identified many of the food items, and Mr. Tamotsu Nakata prepared the figure. All are employees of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

COMMON NAME

The American Fisheries Society (1960:48) lists the common name of *Phtheirichthys lineatus* as "slender suckerfish." *P. lineatus* is an uncommon or rare fish, however, and no one of my acquaintance applies this rather arbitrary name to it. In Honolulu, *Phtheirichthys* is usually called "lousefish," a name used earlier by Jordan (1907:680). "Lousefish" is used throughout this report.

ATTACHMENT

The data in Table 1 were grouped to reflect the various objects to which lousefish attached. Most small fish (ca. 40–130 mm standard length) came from essentially motionless objects: buoys, baits, and large dead fish hanging from the longline gear that caught them. One lousefish was attached to a living porcupinefish, *Diodon hystrix* Linnaeus, a notoriously slow swimmer. Lousefish have been reported from other slow swimmers including turtles (Menzies, 1791:187), barracuda (Jordan and Evermann, 1898:2268; Schultz, 1943:256; Smith, 1950:341), and large groupers (Smith, 1950: 341). It is difficult to accept Jordan and Evermann's statement (1898:2268) that lousefish occur on spearfishes.

Six specimens were free-swimming when collected, including the three largest ones which were attracted to a submerged light at night. One of the latter was kept alive in the ship's baitwell for 10 days, during which time it was occasionally seen to attach to the tank walls for 1 or 2 seconds at a time. Later it was transferred to a circular plastic swimming pool, 23 ft in diameter and 4 ft deep, which was supplied with running salt water. Here its attaching and other behavior were observed for two 1-hr periods each day for 25 days.

The captive lousefish attached only under two conditions: when I entered the pool or when it had been fed to satiety. It was necessary to clean the pool's windows and drain-strainers every few days; when I entered the water to do this work, the fish abruptly ceased swimming and attached to the pool's bottom or side. It usually remained attached for a few minutes and then darted toward me, especially if I was swimming. When I swam, it accompanied me around the pool, staying about 1 ft from my bare feet, but making no effort to attach to me.

The lousefish was fed once or twice a day. Feeding was avid to the point of greediness, the satiated fish having a bulging belly and cheeks, and usually being unable to close its mouth. In this state its swimming movements appeared to be hampered. It sank to the pool's bottom and did one of three things: either it swam slowly back and forth with a great deal

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[1] Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received March 31, 1966.

TABLE 1

CAPTURE DATA FOR *Phtheirichthys lineatus*

DATE	LATITUDE	LONGITUDE	SEX*	STANDARD LENGTH (mm)	HOST OR HABIT
2/ 1/57	13°44′ S	110°02′ W	?	55.7	dip-netted beneath night-light
10/ 5/62	19°12′ N	156°05′ W	–	256	dip-netted beneath night-light
10/ 5/62	19°12′ N	156°05′ W	M	273	dip-netted beneath night-light
9/29/51	21°24′ N	158°15′ W	F	300	dip-netted beneath night-light
10/30/58	04°58′ S	149°52′ W	?	32.8	caught by British Columbia trawl
11/ 1/58	05°00′ S	149°58′ W	?	48.4	caught by British Columbia trawl
8/28/56	11°23′ S	134°32′ W	?	46.0	in *Thunnus albacares* stomach
7/18/50	03°00′ S	171°22′ W	?	53.0	attached to longline buoy
7/20/60	11°30′ N	161°21′ E	?	53.2	attached to longline buoy
8/26/56	13°26′ S	132°16′ W	?	54.0	attached to longline buoy
7/18/50	03°00′ S	171°22′ W	?	56.1	attached to longline buoy
2/ 7/63	17°57′ N	149°39′ W	?	51.3	attached to longline bait (squid)
2/23/63	20°41′ N	150°06′ W	?	55.5	attached to longline bait (squid)
2/ 7/63	17°57′ N	149°39′ W	?	58.9	attached to longline bait (squid)
7/31/63	21°24′ N	149°51′ W	?	61.6	attached to longline bait (squid)
2/ 6/63	18°16′ N	149°46′ W	?	92.4	attached to longline bait (squid)
8/27/56	12°16′ S	133°20′ W	?	44.0	attached to longline bait (fish)
7/24/63	14°22′ N	149°58′ W	–	81.3	attached to longline bait (fish)
7/10/63	14°24′ N	150°11′ W	–	112	attached to longline bait (fish)
5/ 5/62	02°09′ N	157°13′ W	?	48.9	attached to dead *Thunnus albacares*
2/ 6/63	18°16′ N	149°46′ W	F	126	attached to dead *Coryphaena equiselis*
8/29/62	Kahana Bay, Oahu		?	59.6	attached to living *Diodon hystrix*
7/18/50	03°00′ S	171°22′ W	?	48.6	unknown
3/15/59	14°49′ N	150°12′ W	?	60.2	unknown

* (?) = sex could not be determined; (—) = specimen not dissected.

of lateral wriggling, or it rested on the bottom with its belly down, or it attached to the pool's bottom or side. Each of these activities lasted as long as 15–20 minutes and appeared to represent a post-gorging rest. Sometimes the stuffed fish would regurgitate part of its meal and revert to swimming. Although bottom-resting was the most common post-feeding act, it is unlikely that this could happen in nature because substrates suitable for resting would not be available. If satiation resulted in such a temporary weight gain or such a loss of swimming mobility that a resting place was necessary, it is probable that a wild fish would never venture far from its attachment site. It is also probable that full meals are rare in the wild.

The lousefish made no use of its fins when resting on the bottom or attached. The large caudal was collapsed about its long central rays, the dorsal and anal were folded against the body, the pelvics were depressed, and the pectorals were semiflexed.

SWIMMING

Except for the situations noted above, the captive lousefish swam constantly in either of two patterns. More commonly it swam back and forth across the pool, passing near the center each time. In a round trip, one passage was at the pool's mid-depth (2 ft) and the return just above the bottom (4-ft depth). On the mid-depth trip the fish's attitude was normal (disk up); on the bottom trip it was inverted (disk down). During the short vertical connecting trips, the disk faced the tank walls. The fish oriented to the walls or bottom when 6–12 inches from them. Less commonly it circuited the pool's periphery on its side, with the disk facing the pool wall.

Some differences in swimming method were noted within these patterns. When the fish was swimming with the disk up, the head was essentially horizontal, the body axis hung about 8° below the horizontal, and the pectorals were well extended. When it swam inverted, the head was again horizontal and the trunk axis dipped about 8° below the horizontal, but the caudal fin touched the pool bottom and the pectoral fins were folded. When it swam on its side along the wall, the pectorals were half folded but the caudal did not touch the wall. The inverted fish kept its head about 1½ inches above the bottom, but when swimming on its side 2 or 3 inches separated the head and the wall.

In most swimming the caudal fin was well expanded to a rhomboidal or oval shape, the pelvics were folded, and the dorsal and anal fins were only partly erect. The fish's sinuousity was impressive, as it could execute 180° turns in a circle about 6 inches in diameter. The pectorals and sometimes the pelvics were erected when the fish changed course or its plane of swimming, and also when it had just been fed to satiation. In addition, the gorged fish occasionally swam at an angle of 15° to 35° from the horizontal.

Swimming speeds were calculated for each of the three swimming attitudes and for the hungry and fed fish. Data were obtained by timing the fish as it swam between reference points on the pool's sides. Speed data are given in Table 2. In contrast to normal and inverted swimming, side-swimming when satiated was observed only once. The values given are the extremes of a number of readings. The loss of speed after feeding was marked but of short duration. Unfortunately, the only data showing this change relate to tail-beat frequency, not to speed. Tail beats were counted at 66/minute immediately after feeding, but suddenly increased to 78 and 84 beats/minute 11 minutes later.

TABLE 2

SWIMMING SPEED FOR THE LOUSEFISH

STATE OF FISH	SWIMMING ATTITUDE	RANGE IN SWIMMING SPEED (ft/sec)
Not fed for 7–12 hr	normal	1.61–2.05
	inverted	1.88–2.04
	on side	1.41–2.21
Fed to satiety	normal	0.80–1.61
	inverted	0.87–1.32
	on side	1.15–1.39

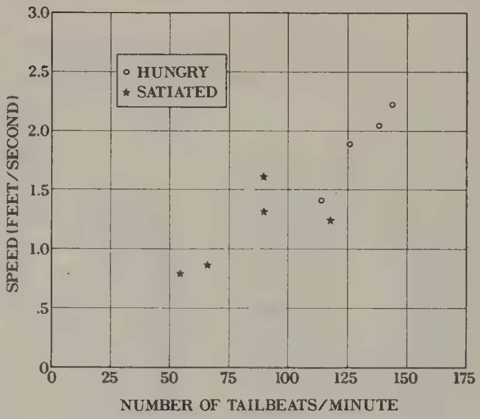

FIG. 1. Speed versus tail-beat frequency in the lousefish.

Figure 1 shows the relation between speed and tail-beat frequency. Speed and tail-beat data were obtained simultaneously as the fish transited the pool. The number of beats per minute ranged from 48 to 144. No speed estimate was obtained for the 48-beat value, which occurred 2 minutes after gorging and 1 minute before the fish sat on the bottom.

RESPIRATION

While the lousefish was swimming, its mouth was always open and no opercular movements were detectable. In this respect it resembled *Remora remora* (Linnaeus), which ceased opercular pumping under conditions of optimum, if artificial, water flow over the gills (Strasburg, 1957). The speed range (or the flow rate) observed for the hungry lousefish (1.41–2.21 ft/sec), however, was more than twice the range (0.75–0.88 ft/sec) judged optimal for *R. remora* (Strasburg, 1957).

When gorged, the lousefish usually sat on the bottom or attached. Its mouth remained open and opercular respiratory movements were conspicuous. The well-developed tongue was alternately pressed to the mouth's roof and returned to its bed, in a rhythm keyed to the opercular movements. Sometimes the fish oriented to face the weak current at the pool's inlet. The number of respirations per minute ranged from 84 to 120—a much lower range than for *R. remora*, which had from 203 to 244 respirations per minute when attached but unfed (Strasburg, 1957). Stuffing the digestive tract with food possibly inhibits the respiratory rate on some mechanical basis. Once when the lousefish fed until it bulged, and then attached to the bottom, it had a rate of 84 respirations per minute. Six minutes later, when it regurgitated four cubes of shark flesh, the rate increased to 114 respirations per minute.

FOOD AND FEEDING

The results of stomach analyses of four lousefish were presented in an earlier paper (Strasburg, 1959:246). It has since been possible to examine 16 more stomachs and obtain better definition of the scope of the diet, and also to observe the feeding behavior of a living specimen.

Of the 20 lousefish stomachs examined 2 were empty. The balance contained mostly planktonic crustaceans, especially small and larval forms. The crustaceans and the number of stomachs in which they occurred were as follows: hyperiid amphipods (1), unidentified amphipods (6), crab larvae (2), unidentified decapod larvae (1), stomatopod larvae (2), Euphausiacea (1), Mysidacea (1), Ostracoda (3), unidentified crustacean fragments (3), and the following copepods: *Candacia pachydactyla* (5), *C. aethiopica* (2), *Candacia* sp. (1), *Scolecithrix danae* (1), *Euchaeta* sp. (3), unidentified calanoids (3), *Sapphirina* sp. (1), *Oncaea* sp. (1), and unidentified cyclopoids (1). Also, 2 stomachs contained fish flesh and bones, and 2 had small flakes of rusty iron.

None of the food species is parasitic, and it is thus unlikely that the lousefish is a cleaner, in contrast to most other echeneids (Szidat and Nani, 1951:413; Maul, 1956:14; Strasburg, 1959:246). Instead, it appears to feed rather selectively on planktonic animals, especially on such conspicuous creatures as the black-and-white copepods *Candacia pachydactyla* and *C. aethiopica,* the iridescent blue copepod *Sapphirina,* and large stomatopod larvae. Rust flakes from the fishing vessel probably were ingested because they were relatively conspicuous. Mysids had been eaten only by the 59.6-mm lousefish attached to a living *Diodon hystrix* caught in Kahana Bay, Oahu. Mysids abound in this shallow bay, and the fish had gorged on 41 of them.

The captive lousefish was fed small cubes of bread, shrimp, or shark flesh once or twice a day. Presentation of food was preceded by a cue (described below) and continued until the offerings were ignored. The fish reacted to food particles from a distance of about 3 ft; the water was very clear. It refused particles lying on the bottom, and preferred to feed on sinking food pieces near the surface. Pieces less than about 3 mm in greatest dimension were ignored in favor of larger ones (up to about 1 cm in greatest dimension). The 3-millimeter pieces were "inhaled" without noticeable jaw movements, whereas those in the 7- to 10-mm range were gulped with conspicuous jaw action. As noted earlier, the fish was a greedy feeder and ate until its belly and cheeks bulged. A full meal required 3 or 4 minutes to consume. When fed once a day for 3 successive days, the volume of shark flesh eaten per meal was 5.1, 5.0, and 2.6 cc. On the last day the fish also ate bread crumbs whose volume had not been measured.

The lousefish was accidentally placed in the wrong pool at first, and for a time I planned to recapture it by dip net for transfer elsewhere. It was necessary to condition the fish to the dip net, for its earlier capture had made it wary. A dip net was placed in the pool before each feeding, and food was offered over the net so that the fish had to swim above the meshes to feed. On the third day of this procedure (the fifth feeding) the fish swam slowly but directly to the net when it was placed in the pool. At the next feeding it dashed immediately to the net, and continued to do so whenever the net was shown. Because it proved unnecessary to transfer the fish, this conditioning went for nought. The fish was subsequently trained to come to the feeding area when the water's surface was slapped with the hand.

COLOR AND COLOR CHANGE

A description of the life colors of the lousefish could not be found in the literature and is therefore presented here. In sunlight the dorsal surfaces of the head and body are navy blue and the ventral surfaces are white. In shade the navy blue often appears as velvety black. Separating these contrasting colors are three lengthwise stripes along the sides. The upper stripe is narrow and light blue, the middle is broad and black, and the lower is narrow and silvery white. The light-blue stripe commences on the upper snout (where it meets its fellow), touches the upper edge of the eye, and continues thence to the caudal base. The black stripe runs from the snout through the eye to the caudal base, and expands on the caudal fin so that the fin is black except for narrow white dorsal and ventral margins. The silvery-white stripe runs from the rictus to the lower edge of the eye and thence along the lower mid-side to the caudal base. The dorsal and anal fins are black basally and margined with white anteriorly. The pectorals and pelvics are plain blackish.

This color was characteristic of the captive lousefish during its first 7 days in the swimming pool. Thenceforth its ventral surface gradually darkened, changing from white to gray-spotted (eighth day) to uniform gray (ninth day) to gray-black (tenth day). Subsequently the color of its undersides fluctuated between gray, deep slate blue, and black, there being no apparent relation between color and incident light or fish activity. Frequently, however, the color of the undersides was lighter just after feeding. Sometimes the back and the base of the dorsal and anal fins were the same color as the undersides. The three lateral stripes were unvaryingly the same. By the twenty-first day the fish's dorsal and ventral surfaces were both jet black, and no further changes were observed. When the fish was preserved after 25 days, it retained its melanistic coloration in alcohol.

During the lousefish's 25-day confinement, the color of the pool walls changed markedly as the diatom *Melosira* proliferated from essentially nothing to a growth 2 inches thick. The fish's gradual color change paralleled this growth. The darkening may have been caused by a general increase in the amount of melanin. On the other hand, a faculty for rapid color change has been reported for *Echeneis naucrates* (Beebe and Tee-Van, 1933:222; Nichols *in* LaGorce, 1939:163; Sanborn, 1932:89; Townsend, 1927:171) and for *Remora remora* (Maul, 1956:50, 66), and thus it is possible that the observed changes were highly transitory.

Another explanation for this color change derives from observations on echeneids which regularly attach. These fish have been stated either to lack countershading (Cott, 1940:43; Pincher, 1948:283) or to have reversed countershading (Norman and Fraser, 1949:176). A lack of countershading supposedly results from a failure to maintain constant orientation to a light source; a reversal of countershading arises from the fact that the echeneid's belly is usually more brightly illuminated than its back. The first explanation possibly fits the color change described above for the lousefish. When captured it had normal countershading, but began to lose it after a period in which swimming was often inverted or on the side. When free in the pelagic environment the lousefish presumably swims in a normal attitude.

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THE ROLE OF RESEARCH IN THE PRESERVATION OF ESTUARIES[1]

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It is the purpose of this report to take note of man's changing attitude toward management of the Nation's coastal waters and to focus attention upon the role of biological research in conserving estuarine nurseries of marine organisms. In considering this subject some aspects of estuarine management in the Gulf of Mexico are discussed, and emphasis is placed on the case history of one hydraulic engineering proposal in Florida which was modified principally because scientists were on hand with appropriate data. Many of the estuarine management problems in Florida closely resemble those in other states.

NATIONWIDE STATUS OF ESTUARIES

Until the war years of the 1940's, alteration of the Nation's tidelands and estuaries had not become a serious problem. Although sensitive observers foresaw progressive deterioration of coastal areas in years to follow, no one truly realized the degree to which unrestrained coastal development would jeopardize land and water resources along the edge of the Continent.

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[1] Contribution No. *33*, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida.

Since World War II the population of the United States has risen from 142,000,000 to 195,000,000; our society has become the most affluent in man's history and the industrial output, staying abreast of our needs, wishes, and demands has reached a point completely inconceivable a few years ago. The United States has doubled its manufacturing capacity in the last 15 years; the output from factories grew as much between 1951 and 1966 as it did in the first 150 years of the Nation's industrial history. About 30 percent of our population lives within 50 miles of our coastlines, and this, of course, has put great pressure on coastal areas.[2] This belt includes all of the estuarine zones.

To accommodate this mass of humanity and its activities, physical and chemical alteration of the estuarine zone began, and was far advanced before marine conservationists took serious notice. Pollution, dredging and filling, building of waterfront homesites, and draining of marshes began in earnest 15 or 20 years ago. Suddenly in the past 5 years we have been able to envision the day when biological production of marine animals and plants might be reduced to insignificance.

Engineering projects have been opposed occasionally during the ravage of coastal waters but most objections have been unsuccessful for a variety of reasons. In many instances state legislation was insufficient for the protection of estuaries; ecological information describing the value and dependence of the marine resources on coastal zones was lacking; and the public was uninformed and apathetic. States have the authority to manage their submerged lands and the fisheries. Some of them have sold those lands and allowed major physical changes in bottom configuration. Some have allowed toxic and nutritional effluents to pour into streams and bays without concern for biological damage.

In view of the number of recent estuarine symposia, panels, and research papers on the vanishing shoreline, a detailed restatement of the national estuarine problem would be redundant. Cain (1966a) and McHugh (1966) have described the biological, economic, and social complexity of estuarine management remarkably well. They have outlined the present status of the problem, the dangers of allowing it to go unchecked, and the recent and gradual turning from ignorance and apathy to a new consciousness.

GULF OF MEXICO ESTUARIES

As the last relatively undeveloped shore, marginal lands of the Gulf of Mexico are now receiving unprecedented attention by industrialists, home builders, and fishermen. Not many years ago human activity was comparatively limited on the Gulf Coast; the population was sparse, and the fishing industry contributed little to the gross national product. Today, the population remains small in comparison with that in most coastal sections of the United States, but it, too, is beginning to enlarge rapidly. The wilderness characteristics of much of the Gulf Coast are increasingly attractive to vacationers, sport fishermen, and permanent residents. Petroleum, shipping, and other industries are increasing with the population and the heightened activity in the coastal waterways. Simultaneously, the importance of marine resources is increasing. Now the fishing industry of the Gulf States harvests 1.4 billion pounds of fishery products annually—about one-third of the nation's catch, valued at $114,000,000 (Lyles, 1965). This fact is evidence that scientists and conservationists must find means to protect the estuarine zone which is responsible for most of the commercial fishery product in the Gulf (Sykes and Finucane, 1966). The five states that lie on the Gulf of Mexico encompass some 14 million acres of estuarine and marshland complex (Sykes, 1964). A recent survey[3] has shown the failure to maintain Gulf estuaries at a high level of biological production. Four percent or 540,000 acres have been totally removed from a biologically productive status or heavily damaged in the immediate past. Once again, natural features of estuarine waters are endangered by the enterprises of man.

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[2] McBroom, James T. Remarks at a meeting of the Mason-Dixon Outdoor Writers Association, Washington, D. C., February 18, 1967.

FLORIDA ESTUARIES

Some 1,900,000 acres of estuarine area lie within Florida, of which 390,400 acres (19.6 percent) have declined in biological productivity or have been completely taken out of production. The damage resulted principally from the construction of fills in bays (Figure 1). The size of Boca Ciega Bay, an arm of Tampa Bay, has been reduced by 20 per cent from filling for residences. Secondary damage has been inestimable on bottoms from which fill material was dredged and over luxuriant beds of sea grass and associated algae. Severe siltation and turbidity have decimated fishes and invertebrates.

Filling in Boca Ciega Bay and other coastal areas of Florida requires purchase of submerged lands and then permits from the County, State, and finally the U. S. Army, Corps of Engineers. In the past these regulatory measures have been more a formality than an obstacle to land developers. Recent events have captured the attention of legislators and public and appear to mark a change in attitude toward the sale of submerged land and the issuance of permits.

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[3] Unpublished data, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida.

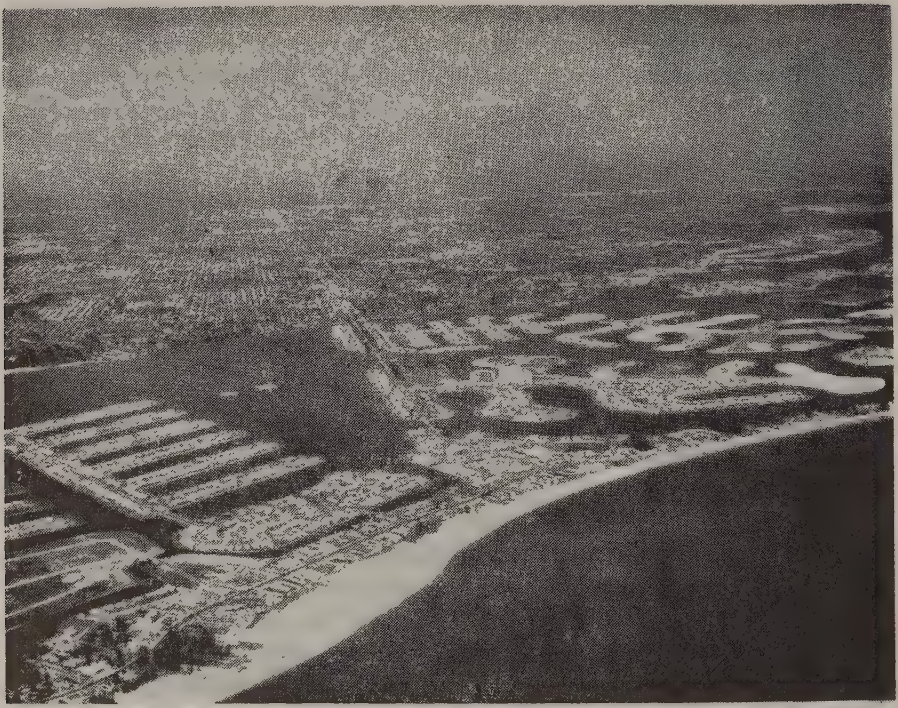

Figure 1. Aerial view of a portion of Boca Ciega Bay, Florida. St. Petersburg in the background and the Gulf of Mexico in the foreground. (Photograph courtesy of Airflite, St. Petersburg, Florida.

A SPECIFIC DREDGE-FILL CASE IN FLORIDA

The Bureau of Commercial Fisheries does not engage directly in local controversies. Our investigation of estuarine ecology, however, serves to document the biological status and value of coastal waters and to make results available to other agencies and the public. For example, data supplied by the Bureau of Commercial Fisheries Biological Laboratory at St. Petersburg Beach, Florida, were instrumental in blocking the proposed Tierra Verde fill, which received national attention (Boyle, 1964). Less damaging plans were subsequently submitted for consideration.

In 1957, the Tierra Verde Corporation applied for permits from the County, State, and U. S. Army, Corps of Engineers, to dredge and fill within a 1200-acre area of lower Boca Ciega Bay. At that time it was generally customary for agencies ruling on proposals to concur with decisions of the local ruling body—the County—and to grant subsequent permits should one be given at that level. A public hearing on the proposal was held before the County Commission in 1957. The partial record on hand shows that attorneys represented the applicants and the objectors.

The available testimony of particular interest to scientists and conservationists consisted of statements by consulting biologists representing the applicants. These witnesses in essence agreed with each other that the massive dredge-fill project would have no adverse effect on the natural resources of the area and that the benefits from such a project would totally outweigh any minor loss that might be incurred.

One consultant indicated that some shrimp feeding grounds but no major sport fishing areas would be lost. It was stated that deep water and edges would be formed in borrow areas and that new fishing grounds would be provided. "The deep holes would provide havens, resting places, and concentration areas for many species of fish which now are not commonly found in the area; for example, trout, channel bass, redfish, sheepshead, and other fish generally found in dredge holes. All along the Gulf Coast where there have been dredging operations of this type, there are good fishing holes following such dredging operations." Another support given for an increase to sport fishing value was the greater potential accessibility of fishing areas to fishermen.

Statements by another biologist consultant to the applicant held that shallow flats were sometimes exposed or at least the water was very shallow and therefore relatively barren of marine life. It was argued that animals came and went with changes of tide and that they were also exposed to extreme temperatures. The consultant added that he "would not expect" to find extensive grass beds or suitable habitat for young marine animals in such areas.

Apparently no testimony based on biological studies in the area was given in behalf of conservation interests since no record of it can be located. Conservation agencies and the public did object to the proposal, but their views failed to impress governing authorities as much as other projected values. This attitude is partially understandable because the present trend toward conservation of estuaries is too recent to have been strongly in effect in 1957 and, generally, biological research in estuaries was more closely related to autecology than synecology. Even though bay-filling projects were well under way at that time, the magnitude and damages wrought to ecosystems did not generally reach a critical or noticeable point until a few years later. It has been mentioned (Thompson, 1961) that bay filling is comparable to balding in the human male. Hairs drop unnoticed one at a time over a long period; suddenly, approaching baldness is noted with an alarmed awareness. So it is with bays and an awareness of their condition.

Upon issue of County, State, and Federal permits the developing corporation established approximately one-half of its approved fill. In the years between completion of this portion and initiation of plans to complete the total development, the Bureau of Commercial Fisheries Biological Laboratory was established at nearby St. Petersburg Beach—an act which was to have an effect on further operations of the developer. News releases describing the projected development early in 1964 stated that dredging and filling of 500 acres would be started immediately. Doubting that legal engineering permits were still in effect at all governing levels, we sent letters of inquiry to the Water and Navigation Committee of the Pinellas County Commission and to the U. S. Army Corps of Engineers. The Federal permit, granted in 1957, had expired in 1960, and whether or not one was still valid at the county level seemed doubtful. The announced intention of the corporation to dredge and fill immediately, and its haphazard attitude toward the status of permits may convey some notion of the power of bay-fill developers even as recently as 1964.

Finally, it was decided that a county permit was still in effect but the County Commission in the light of recent biological findings by the Bureau of Commercial Fisheries Laboratory and mounting public pressure agreed that a new public hearing was in order at the local level. Estuarine ecological research by the Laboratory had been performed within the boundaries of the proposed Tierra Verde development before the renewed plans for additional filling. After those plans were announced, intensive surveys were initiated to detect any changes in the biological system which might have occurred in the interim. No appreciable changes in fauna or flora had taken place between our periods of investigation.

The area supports an unusually luxuriant growth of turtle grass (*Thalassia testudinum,* Figure 2). This finding was in direct contradiction to statements of the consultant at the earlier hearing. Turtle grass is widespread in the shallow areas of the Gulf of Mexico, the Florida Keys, the Bahamas, and the West Indies. It is of great ecological importance as a primary producer of food and as a habitat for marine animals. Stephens (1966) estimated that a square mile of turtle grass near Miami contained 235 million shrimps and 95 billion mollusks. He reiterated the ecological principle that many of these animals, too small to serve as food for man, are of great importance as food for finfish and crustaceans. Additionally, many of these species, such as the shrimp, are merely the young of those which are useful upon maturity as human food.

The grass flats of Tierra Verde are partially exposed at low tide as indicated by the consultant who testified in behalf of the original permit. Although the consultant "would not expect" to find the flats to be suitable habitat for young marine animals they are actually

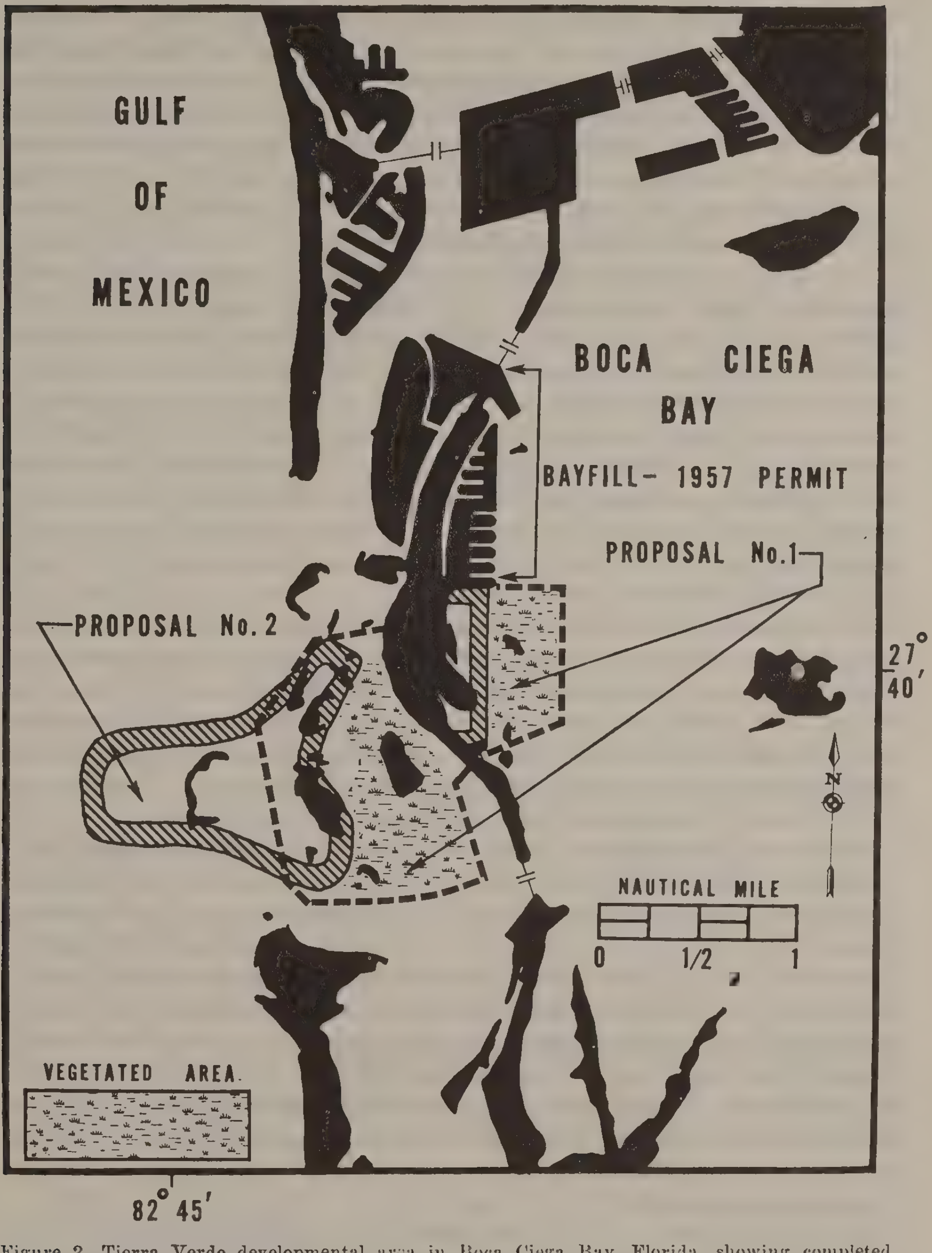
GULF
OF
MEXICO
BOCA CIEGA
BAY
BAYFILL– 1957 PERMIT
PROPOSAL No.1
PROPOSAL No. 2
27°
40′
N
NAUTICAL MILE
0
1/2
1
VEGETATED AREA
82° 45′

Figure 2. Tierra Verde developmental area in Boca Ciega Bay, Florida, showing completed portion, fill area proposed initial design, and final alternate proposal.

teeming with marine life as Stephens (1966) found. Our samples indicated an estimated 224 grams (dry weight) of invertebrates per square meter within the area (Taylor and Saloman, unpublished manuscript).[4] In epibenthic studies of the same area, Saloman (1965) showed that one of the abundant marine animals using the grass flats as a nursery was the pink shrimp, *Penaeus duorarum*. This and other species of shrimp constitute the most valuable element of Gulf of Mexico commercial fisheries. On the basis of historical data, Saloman (1965) also demonstrated a direct correlation between reduction in quantity of pink shrimp in Tampa Bay and earlier destruction of grass beds by dredging and filling.

Not only are the grass beds used as a shrimp nursery, Sykes and Finucane (1966) found that 17 of the most valuable sport and commercial species of finfish in Gulf catches inhabit the grasslands as juveniles. Whether or not adults of sport fish use inter-finger channels for "havens and resting places" as stated by consultants seems beside the point if grass beds used by juvenile sport fish are destroyed to create deep-water areas. Anchovies, mullet, and tidewater silversides are the most commonly caught fishes in inter-finger canals, and benthic studies have shown that deeply silted bottoms support only meager infauna and epifauna, and no macroscopic plants (Taylor and Saloman—see footnote 4).

On request of County Commissioners these data were entered in the record of the hearing as indicative of the importance of the area as a marine nursery. The value of Gulf of Mexico commercial fisheries was shown, and the dependence of commercial species upon the nursery was discussed thoroughly. Apparently the area to be filled was accepted as important for something greater than the "love life of fiddler crabs," as one real estate developer had termed it.

The sardonic reference to fiddler crabs and the lighthearted attitude about the value of the marine resources were not well received. Among other miscalculations of the developer such unbecoming statements were to prove unwise in view of the adverse public sentiment and the intelligence of the considerable number of people attending the hearing. Objections to destruction of the nursery were presented by representatives of the Audubon Society, the Wilderness Society, the Isaac Walton League, the League of Women Voters, the St. Petersburg Garden Club, and owners of property in the vicinity of the proposed land fill. Also represented, in addition to the Federal agencies and the Florida Board of Conservation, were local university scientists and students.

Such large and dynamic representation at hearings on resource matters was not typical on the west Florida coast in 1964 and may be attributed to fast-growing indignation toward the destruction of estuaries. This hearing probably will prove to be a turning point in the management of submerged lands of Florida; it might have been effective even if the opposition had lost its case.

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[4] Taylor, John L., and Carl H. Saloman, "Some effects of hydraulic dredging and coastal development in Boca Ciega Bay, Florida," on file at Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida.

Regardless of the lengthy hearing and the expert testimony containing less than the usual emotion, conservation forces very nearly lost the estuarine nursery. The contest was decided by the tie vote of four County Commissioners; two for and two against. The permit needed a majority. We venture to hold that the combination of biological data and the testimony of conservationists were responsible for the two votes which rejected issuance of the permit.

For some months after the decision, opposing civic groups feared that a Federal permit might still be issued for completion of the project. It was feared also and, in fact, seemed possible that the development corporation would bring suit on the grounds of incompetent testimony (testimony was not sworn), violation of the owner's right to use his property, or other alleged irregularities in procedure.

After several months the developer requested a meeting with personnel of the Bureau of Commercial Fisheries and the Florida Board of Conservation to attempt a resolution of differences. It was suggested that we design an alternate real estate development at the same location that would satisfy needs of the marine resource. The spokesman for the corporation indicated that negotiations and compromises with marine scientists and governmental authorities would be more expedient and practical than court procedure. As far as Federal authority is concerned, he was informed it did not include the designing of land fills but that it did include an inspection and opinion on any alternative plan which might be submitted.

In a few weeks the developer submitted a revised plan for consideration. It was not acceptable to us, however, principally because it continued to express intention of covering a large portion of the existing *Thalassia* beds.

Finally another proposal was submitted in which the intended land mass would be shifted away from submerged vegetation (Figure 2). After examination of the plan by personnel of the Bureau of Commercial Fisheries, the Bureau of Sport Fisheries and Wildlife, and the Florida Board of Conservation, a concensus was reached that no further objections would be raised to the proposal by these agencies provided that:

1. The area would be diked before filling for the prevention of siltation on grass flats.
2. All fill material for the eastern side should be dredged from within the designated fill area.
3. Channels should be of adequate width and depth to accommodate small boats.
4. County and State authorities would be notified before the start of

the dredge-fill operation.

5. Piling bridges or flow-through causeway sections should be constructed to provide for estuarine circulation.

6. The above stipulations should appear on the developer's application to the U. S. Army, Corps of Engineers.

After assurance was given that official conservation agencies would offer no further objection to the alternate permit, the next step for the corporation was to determine whether its submerged land could be exchanged for a similar acreage adjacent to its existing property. At this date we have received no official information on prospects for the land exchange or on attitudes of local governments toward the issuance of a dredge-fill permit.

If a formula for resource protection resulted from this case, its components include findings of biological research, willingness of scientists to disseminate their findings in reports and verbally before the public, support of national conservation agencies and societies, and strong assertion of public opinion. In this example results of biological research served as the stimulus in a chain of events which appears to have prevented heavy damage to an estuarine area. After the public and local chapters of conservation agencies began to oppose the project, biological data moved from the forefront and appeared to matter little. Finally, when the permit was rejected the developer realized that the importance of a marine nursery was no small thing. Then, scientists were consulted in an effort to devise the least objectional method of developing a land mass.

This long and tedious method of protecting small sections of estuaries is not necessarily recommended for all situations. A similar procedure is presently being followed, nevertheless, in many situations in Florida. The piecemeal approach consumes too much time and effort of scientists and citizens who are determined in their opposition to the loss of estuaries. The risk of this loss is still too great.

Even when requirements of the marine resource are essentially met, other items need consideration. Often altered circulation can cause erosion, and dwellings built on new land masses are frequently exposed to hurricanes and sea storms. Little attention is paid to water quality, a factor closely related to biological production, recreation, and public health. Nevertheless, the method is more successful than the emotional approach so often used formerly in public hearings and circulated petitions. The voice of conservation becomes stronger when scientific documentation of natural processes in the estuary is added. The argument is no longer based solely on the opinion that "hook and line fishing is not as good as it once was" or that the "wilderness atmosphere is being lost." These opinions are important but assertion that a marine nursery contributes to a commercial fishery worth

$114,000,000 annually and that the need is growing for protein from the sea commands attention. The value of biological data under present methods of rendering decisions on dredge-fill permits is unquestionable and essential until those systems change.

Better means should and can be found to guarantee healthy estuaries. Criteria should be established by which states can protect and manage large estuarine zones. State legislation is needed comparable in some respects to the Federal Water Quality Act of 1965. The enactment of such laws would overcome the need of opposing in piecemeal fashion such projects as the one described.

One of the most satisfactory methods of assisting states in conserving their estuaries would be to require a permit for estuarine engineering from the Department of the Interior in addition to the one presently required from the Corps of Engineers. The primary interest of the Corps is the protection of navigational channels—not fish and wildlife. Stanley A. Cain, Assistant Secretary for Fish and Wildlife and Parks, U. S. Department of the Interior (1966b) has stated that the Secretary of the Interior should have a voice in deciding whether publicly owned areas shall be altered for the benefit of commerce and real estate developers, when broader public questions are involved. The requirement of a permit from the Interior Department would not lessen the need for or importance of biological research in estuaries. Sound decisions would continue to be necessary where varying uses of estuaries compete.

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Noncommercial Crabs of the Genus *Callinectes* in St. Johns River, Florida

ABSTRACT: Noncommercial crabs of the genus *Callinectes* were collected in the St. Johns River, Florida, and in the ocean near the river mouth from 1961 to 1963. They were abundant offshore, and, from April to October, were present in the lower 25 miles of the river system. Juveniles 4 to 30 mm wide were found in certain tributaries that also serve as nursery areas for the closely related blue crab, *Callinectes sapidus*. They occurred at salinities of less than 1%. Females spawned in the ocean from March to July and again in October and November.

During an investigation of the blue crab, *Callinectes sapidus*, in the St. Johns River, Florida, the Bureau of Commercial Fisheries also obtained data (1961 to 1963) on the occurrence and biology of noncommercial species of the genus *Callinectes*. Information on these noncommercial forms is very limited (Brues, 1927; Gunter, 1950; Gunter and Hall, 1963; Daugherty, 1952; and Lunz, 1958) compared with that on the blue crab, the only species that grows large enough to be marketed.

Although various species of noncommercial *Callinectes* of the Western Atlantic Ocean have been described (Rathbun, 1930), all could not be identified with certainty until the taxonomy was revised (Williams, 1966). Two species occur along the Atlantic Coast of the United States—a newly described species *C. similis*, from New Jersey to Mexico, and *C. ornatus*, from South Carolina to the southern tip of Florida. Our collections contained both *C. similis* and *C. ornatus*, but since the two species were not distinguished in the field, I refer to them here as noncommercial *Callinectes* or *Callinectes* spp.

The composition of the crab population in the St. Johns River and in the ocean near the river mouth was determined from our collections obtained with a seine (70 feet long) and a trawl (8 feet wide) and from samples of catches by shrimp trawlers. We usually obtained collections semimonthly at selected stations in the river and sampled catches of river and offshore fishermen monthly.

Noncommercial *Callinectes* were abundant, particularly from May to November, in catches by shrimp trawlers off the mouth of the St. Johns River (an area ½ to 5 miles from shore and between Fernandina and Ponte Verde Beaches was sampled, Fig. 1). The largest catches were in May, June, and October when thousands were captured in each tow. Noncommercial *Callinectes* exceeded blue crab in number every month except August and September (the period of peak spawning of the blue crab).

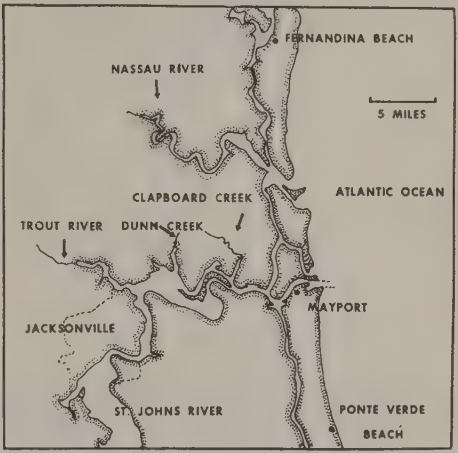

Fig. 1. Lower St. Johns River and adjacent coast.

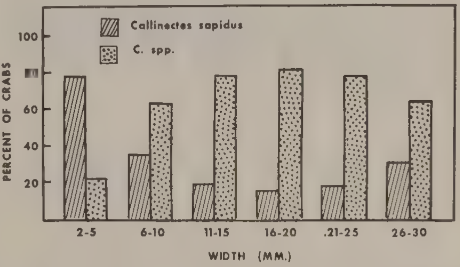

Fig. 2. Relative abundance of *Callinectes sapidus* and *Callinectes* spp., 2 to 30 mm wide, in Clapboard Creek during July–August influx of young-of-the-year *C. sapidus* (2 mm and larger).

Ovigerous females (bearing an egg mass on the abdomen) were taken offshore as early as March. Their number reached a peak in May when approximately 75% of mature females were ovigerous; the percentage decreased to 20% in July. We found no evidence of spawning in August and September, but a secondary period of spawning occurred from October to mid-November. Although adult females were fairly common in the lower river, we saw none in an ovigerous condition. Large numbers of juveniles first entered the catch in the ocean during early fall; the ratio of mature to immature females was 2 to 1 in July samples and 1 to 10 in September samples.

Noncommercial *Callinectes* are typically marine but do occur in the St. Johns estuary. They were captured from April to October from the river mouth to Jacksonville (25 miles), and in the lower 3-mile reaches of Clapboard Creek, Dunn Creek, and Trout River (Fig. 1). From 10 miles upriver to Jacksonville, commercial catches often included hundreds of *Callinectes* spp. and our collections (obtained in 10-minute tows by trawl) contained up to 240 crabs. Almost all of our collections from Clapboard Creek contained *Callinectes* spp. (up to 38 crabs); they were less abundant in Dunn Creek and Trout River. Juvenile noncommercial *Callinectes* often were more abundant than juvenile blue crabs in catches from Clapboard Creek, even during the influx of young-of-the-year blue crabs (2 mm and larger in carapace width, (Fig. 2). Although large numbers of juvenile blue crabs always occurred in Dunn Creek and Trout River, aggregations did not always develop in Clapboard Creek, possibly because of competition from *Callinectes* spp.

Many sizes of *Callinectes* spp. were captured in the river: males ranged from 4 to 140 mm wide and females from 4 to 102 mm wide. Apparently only small crabs ascended the tributaries, however; nearly all returned to the river before their width surpassed 30 mm.

In the St. Johns system, noncommercial *Callinectes* adapted to low salinities and even freshwater (salinity less than 1‰). Nearly all of those captured in the river proper were in salinities greater than 15‰, but many caught in tributaries were in brackish water, and 29 were taken in freshwater.

The occurrence of noncommercial species of *Callinectes* in certain blue crab nursery areas suggests that, at times, there is competition between juveniles of the two forms for food and space.

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Predation by Dolly Varden and Northern Squawfish on Hatchery-Reared Sockeye Salmon in Lake Wenatchee, Washington

RICHARD B. THOMPSON AND DENNIS F. TUFTS

Predation by Dolly Varden and Northern Squawfish on Hatchery-Reared Sockeye Salmon in Lake Wenatchee, Washington

INTRODUCTION

Approximately 3 million sockeye salmon (*Oncorhynchus nerka*) fingerlings, reared at the Leavenworth National Fish Hatchery, were released annually into Lake Wenatchee, Washington, in 1960–65. Before 1960, fingerlings were released into the Little Wenatchee and White rivers, tributary streams of Lake Wenatchee. Fishery personnel observed that Dolly Varden trout (*Salvelinus malma*) and northern squawfish (*Ptychocheilus oregon-*

TABLE 1.—*Occurrence and intensity of predation and mean lengths of sockeye salmon fingerlings in stomachs of predators before, during, and after releases of hatchery fish into Lake Wenatchee, Washington, in 1961*

	Release period											
	Before (18–26 September)				During (27 September–16 October)				After (20–27 October)			
Predator species and sampling gear	Number caught	Percentage containing fingerlings	Fingerlings per predator	Mean fork length of prey (mm)	Number caught	Percentage containing fingerlings	Fingerlings per predator	Mean fork length of prey (mm)	Number caught	Percentage containing fingerlings	Fingerlings per predator	Mean fork length of prey (mm)
Dolly Varden												
Trolling gear	36	30	0.50	62.2	24	100	1.42	94.9	4	0	0.0	—
Gill nets	42	12	0.25	56.0	51	58	1.32	98.0	14	14	0.21	—
Northern Squawfish												
Gill nets	238	<1	<0.01	—	376	32	0.37	97.7	42	2	0.02	—

ensis) actively preyed upon the small salmon before they reached the open lake.

In an attempt to reduce these losses to predators, all hatchery fingerlings in 1960 and 1961 were released directly into the open lake from a mobile planting barge. Of 3 million salmon fingerlings released into the lake between 27 September and 16 October 1961, 1 million had been marked by the removal of the adipose fin and the posterior portion of the right maxillary bone.

The 1961 releases of salmon fingerlings provided an opportunity to appraise the relative changes in the occurrence of juvenile sockeye salmon in predators and to compare the incidence of predation upon marked and unmarked, artificially propagated, fingerlings. The population of sockeye salmon fingerlings in Lake Wenatchee following the releases was composed of wild and hatchery fish. Naturally spawned fingerlings move down into Lake Wenatchee from the spawning streams in the early spring as fry, and migrate out of the lake 1 or 2 years later, also in the spring. The appraisal compared the stomach contents of the two principal predatory fishes captured in the lake, Dolly Varden trout and northern squawfish, before, during and after the releases. Although the Leavenworth Hatchery is no longer propagating and releasing sockeye salmon, investigations are underway elsewhere concerning the rearing of sockeye salmon in lakes and reservoirs. The results presented here, although no longer applicable to the situation described, are pertinent to similar future operations in other waters.

COLLECTIONS AND EXAMINATIONS

Predatory fishes were collected with gill nets and by trolling from 18 September to 27 October 1961. The trolling gear included two 6-ft rods provided with large reels and steel trolling lines. A 1-pound lead sinker was attached at the end of each line. Five monofilament leaders, each 6-ft long, were attached to the main line at 25-ft intervals. Silver and brass spoons and "flatfish"-type plugs were attached to these leaders. The gill nets were 4 ft deep by 120 ft long and of 1¼-inch to 3-inch mesh, stretched measure. In fishing position, the lead lines of the nets rested on the bottom and the webbing was supported upright by the float line. The nets were anchored in depths of less than 90 ft along the shorelines surrounding the areas of the lake in which the hatchery sockeye salmon were released from the barge. The nets were set during mid-day and lifted 24 hours later.

The examination of fishes caught in the gill nets was completed in the field. Fishes caught by trolling were weighed and measured (fork length) in the field; their stomachs were removed, preserved immediately, and examined later in the laboratory. Prey species found in a predator's stomach were identified and measured. The presence or absence of fin and maxillary bone clips was determined for all sockeye fingerlings. No attempt was made to estimate the volume of the stomach contents, because this appraisal was concerned with the occurrence and number of sockeye salmon consumed by predatory fishes.

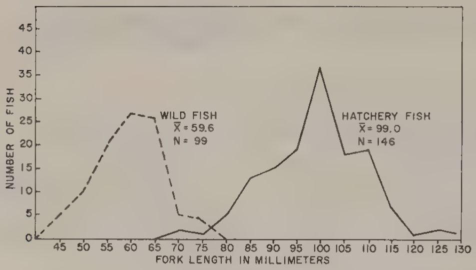

FIGURE 1.—Length-frequency distribution of wild sockeye salmon fingerlings in Lake Wenatchee, 19–20 September 1961, and of hatchery-reared fingerlings before release in the lake 20 September 1961.

SALMON FINGERLINGS IN PREDATOR STOMACHS

Sixty-four Dolly Varden were caught by trolling. Sockeye salmon fingerlings and fish remains, tentatively identified as sockeye salmon but not included in these results, were the only items in the 53 stomachs that contained food. Eleven (30%) of the 36 Dolly Varden caught by trolling in the pre-release sampling period (18–26 September) had preyed on wild fingerlings (Table 1). In the collections of 27 September to 16 October (during releases), all of the 24 troll-caught Dolly Varden contained fingerlings. The stomachs of four fish captured by trolling gear in the post-release period (20–27 October) were empty. Collecting efforts were not constant during these three periods; therefore total catches are not indicative of abundance or availability of the predators.

The average number of fingerlings in Dolly Varden caught by trolling during the pre-release sampling was 0.50 (Table 1). During the release period, the average number of fingerlings per Dolly Varden increased almost three fold to 1.42.

Of the 107 Dolly Varden taken in the gill nets, 82 (77%) had food in their stomachs; sockeye salmon fingerlings and unidentifiable fish remains predominated. Only 12% of the Dolly Varden had eaten fingerlings in the pre-release period, but this percentage increased to 58 during the release period. Similarly, the average number of fingerlings per fish increased from 0.25 in the pre-release period to 1.32 in the period when releases were being made (Table 1).

Of 656 northern squawfish stomachs collected, 355 (54%) were empty. The increase of sockeye salmon fingerlings in squawfish stomachs between pre-release and during-release periods was greater than for Dolly Varden. Less than 1% of the squawfish collected before the hatchery releases contained wild fingerlings. During and immediately following the hatchery releases, this percentage increased to 32. The average number of fingerlings also increased from less than 0.01 per squawfish in pre-release collections to 0.37 per squawfish captured during the release period.

The total number of recognizable marked and unmarked fingerlings recovered from predator stomachs were 27 and 49, respectively. The total hatchery release contained approximately 1 million marked salmon and 2 million unmarked salmon. Chi-square tests, on the basis of these few prey, indicated no difference [$P > 0.10$] between the ratio of marked to unmarked fingerlings planted [1 : 2] and the ratio of these groups found in predator stomachs [27 : 49]. Thus, the susceptibility to predation appeared to be the same for the marked and unmarked sockeye salmon fingerlings in these releases.

The mean fork length of 99 wild sockeye salmon fingerlings collected by beach seine and mid-water trawl on 19 and 20 September 1961, was 59.6 mm; the mean length of 146 sockeye salmon measured at the hatchery before release was 99 mm. The length distributions of the two segments of the Lake Wenatchee fingerling population after releases had little overlap (Figure 1). Hence, identification of the source of prey fingerlings was valid on the basis of size; in addition, one-third of the hatchery-reared sockeye salmon were positively identifiable by marks.

The mean length of fingerlings consumed by Dolly Varden was 62.2 mm during the 18 to 26 September period, and 94.9 mm in the period 20 to 27 October. This difference is similar to that between mean lengths of the known wild and hatchery fingerlings, 59.6 mm and 99.0 mm (Figure 1). An almost complete change from wild to hatchery prey is thus indicated. The occurrence of salmon fingerlings in squawfish stomachs before hatchery releases was so low that a meaningful average length could not be calculated. Squawfish collected during the releases contained enough fingerlings, however, to permit the calculation of a mean length of 97.7 mm. Thus, wild sockeye salmon fingerlings were not a major item of the food of squawfish in Lake Wenatchee; but fingerlings released from the hatchery were available prey for these predators.

After the releases of hatchery fingerlings had been completed, the occurrence of sockeye salmon in predator stomachs declined to about the pre-release level by 27 October. The catch of predator fishes per unit of effort also diminished rapidly after the completion of the releases, possibly because the prey had dispersed throughout the lake and the predators themselves had also scattered.

Samples of predators obtained by the two types of collecting gear demonstrated that the trolling gear was selective for Dolly Varden that had preyed on fingerlings. Pre-release frequency of occurrence of salmon fingerlings in the troll-caught Dolly Varden was about three times greater than in fish caught in the gill nets; the number of fingerlings per fish was twice as high in Dolly Varden caught by trolling as in those from gill nets (Table 1). Occurrences during hatchery releases were 100% and 58% for troll- and gill net-caught Dolly Varden, respectively; number of fingerlings per predator were about equal for the two types of gear. This selectivity could have been caused by: (1) trolling lures that resembled the fingerlings and stimulated attack responses by feeding predators; (2) the difference in fishing locations; or (3) differences in the size of predator fish taken by the two methods (the trolling gear took fish of greater mean lengths). The samples were not extensive enough to measure and evaluate these possibilities.

PREDATOR MOVEMENTS AS INDICATED BY GILL NET CATCHES

Information on different rates of capture of predator fishes in gill nets, set parallel and perpendicular to the shoreline, is added here to illustrate the influence of fish behavior (movement) on collecting results. A higher rate of capture in gill nets is assumed to occur in areas where fish movement is more perpendicular than parallel to the direction of the net. One net was located in an area of the lake where the bottom sloped gradually to 50 ft, another where the bottom sloped rapidly to depths exceeding 60 ft.

The gill nets set on the shallow, sloping bottom captured twice as many Dolly Varden when the net was parallel to the shore as when it was perpendicular to the shore. A general in-and-out movement of the fish in shallower waters was thus suggested.

In the steep-shore set, the catches of Dolly Varden were about twice as great when the net was set perpendicular to the shore as when it was set parallel to the shore. Here, most fish movement was apparently parallel to the lake shore within a depth stratum.

The catch of northern squawfish in the shallow- and steep-slope gill nets was nearly identical, whether the net was perpendicular or parallel to the shore line.

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A NEW HIGH-SPEED TAGGING DEVICE

A new way of applying external tags recently came to my attention. Originally developed for the textile industry, the tags are now available for fishery investigations.[1] Preliminary studies indicated actual or potential advantages over certain conventional tagging systems. This note describes the applicator, tags, methods of application, and preliminary observations.

A series of plastic tags is inserted into a slot in the applicator (Figure 1). The applicator needle is then inserted into the fish at the desired tag site. Compression of the applicator grip activates a spring-loaded piston which drives the T-bar end of the tag through the hollow, slotted needle. In this action the bar of the T is driven lengthwise through the needle, while the monofilament passes freely along the slot. As the needle is withdrawn the bar catches and turns perpendicular to the path of the needle. This turning prevents the tag from pulling out. The next tag is drawn into position when pressure on the applicator grip is released.

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[1] Applicator and tags are available from Floy Tag and Manufacturing Inc., 2909 N.E. Blakeley Street, Seattle, Washington 98105.

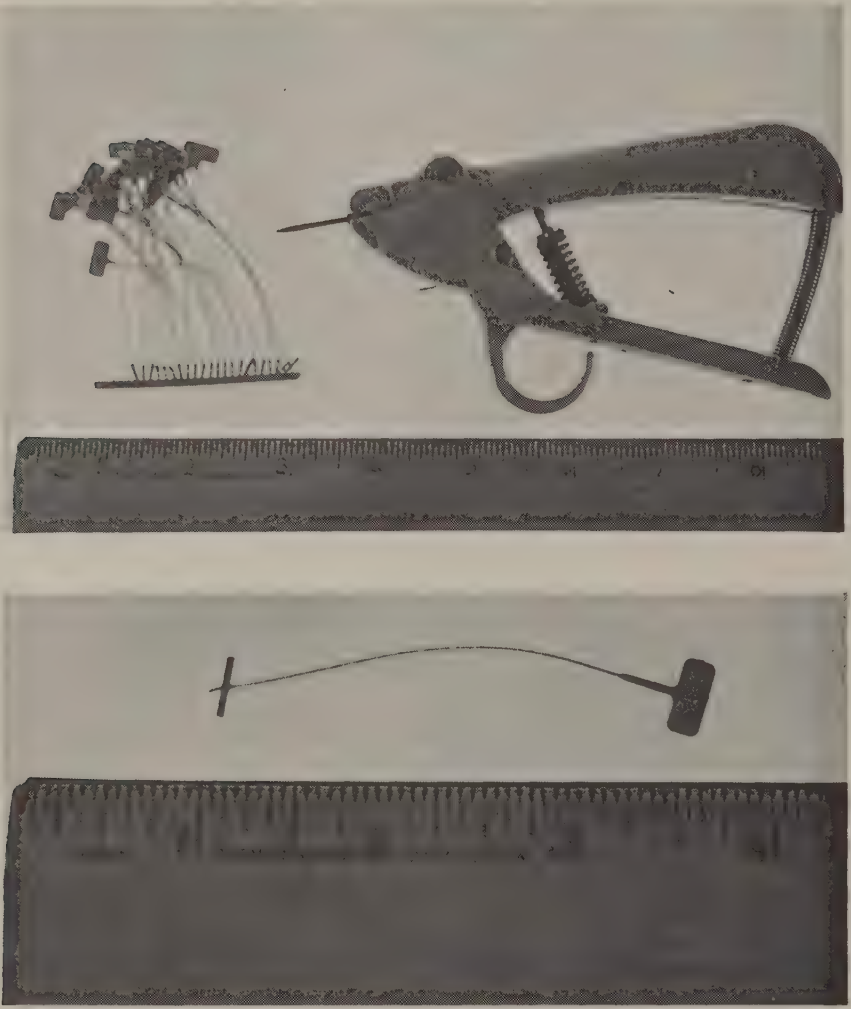

FIGURE 1—Upper: Applicator and series of tags, moulded to the header. Lower: A single tag.

About 24 rainbow trout (*Salmo gairdnerii*) were tagged at two sites (Figure 2): (i) through the dorsal musculature near the dorsal fin and (ii) in the flesh under the dorsal fin. When inserted near the dorsal fin, the needle was angled anteriorly to emerge near the origin of the dorsal fin; the trailing tag body and pennant then held the bar snugly against the skin. When inserted under the dorsal fin, the needle was placed so that the neural spines and dorsal fin interneurals helped maintain the 90° attitude of the bar. Here insertion of the needle slightly deeper than the intended implant point, followed by withdrawal before compression of the grip, allowed easier clearance of the bar from the needle than when inserted less deeply, and freer return of the bar to the 90° attitude.

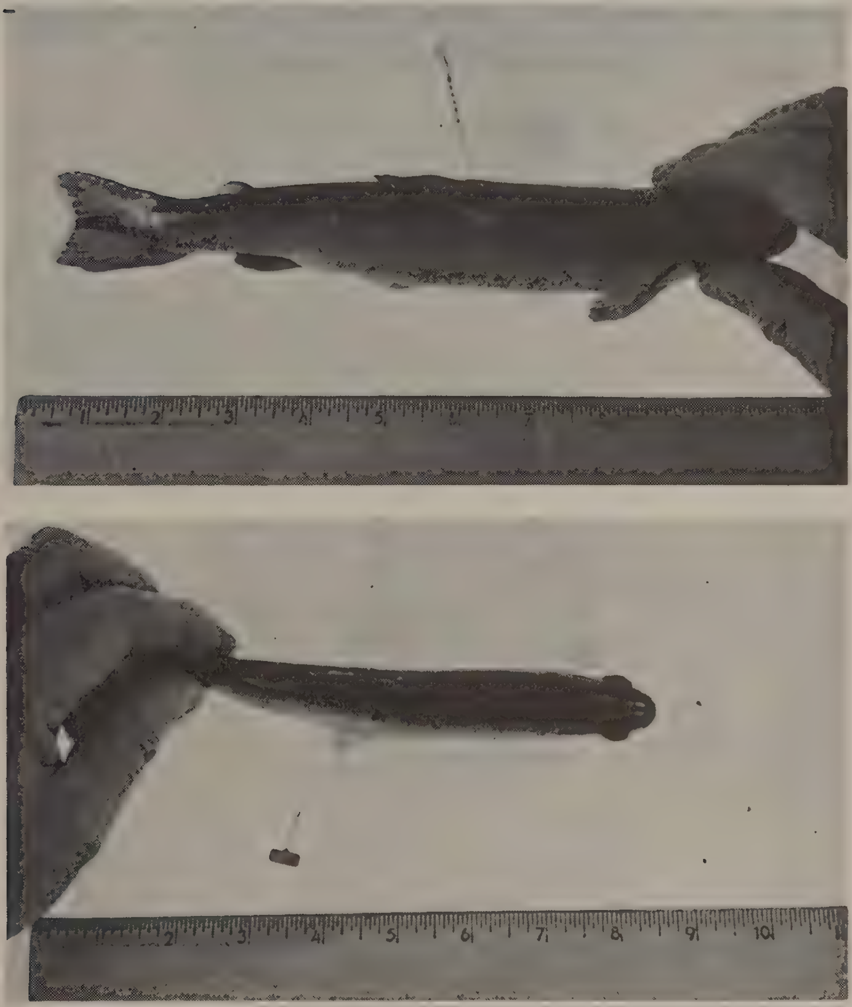

FIGURE 2—Upper: Rainbow trout tagged through the dorsal musculature anterior to the dorsal fin. Lower: Rainbow trout with tag implanted under the dorsal fin.

The rectangular shape of the pennant suggested that the tag might flutter and eventually pull out. Accordingly, tagged fish were placed for observation in a lighted glass flume in which water velocity was 4 feet per second. At this velocity the tag did not flutter, possibly due to the stiffness of the monofilament.

In these tests tag retention was not studied, since the fish were to be sacrificed for other purposes. However, six fish which were still alive after 3 months had retained their tags. A tagging rate of 50 fish per minute was possible. The sample tags were available in several colors, moulded in series up to 100. Colored ''spaghetti'' with labeling was added to some of these. The tags used were 2 inches long, but others from 1 to 5 inches are available. In some cases the pennant was trimmed to alter its shape, but this can also be accomplished by altering the tag mold.—*Kenneth N. Thorson, Bureau of Commercial Fisheries, Biological Laboratory, Seattle, Washington, March 1967.*

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Mitochondriogenesis in Integumentary Cells of the Larval Sardine (*Sardinops caerulea*)

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Mitochondriogenesis in Integumentary Cells of the Larval Sardine (*Sardinops caerulea*)

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A possible mode of mitochondriogenesis has been observed during an investigation of certain integumentary cells believed to have special osmoregulatory functions in the skin of the larval sardine *Sardinops caerulea*. Initially large vacuoles appear in the cytoplasm and cytoplasmic processes invaginate into these to form mitochondrion-like bodies which eventually attain full mitochondrial characteristics. The mitochondrial intermediates appear at the cell periphery, whereas the mature organoids occur in the central cytoplasm.

Previous research on mitochondria has suggested that there are three possible modes of mitochondriogenesis and that these are not necessarily mutually exclusive. First, new mitochondria may arise by the growth and division of preexisting mitochondria. This view is supported by numerous light microscope observations on fixed and living cells and more recently by experiments involving the incorporation of radioactive choline and thymine into mitochondria (*6*, *7*). Second, mitochondria may be elaborated from other nonmitochondrial structures or membranes, i.e., microbodies, endoplasmic reticulum, plasma, and nuclear membranes (*3*, *4*, *8*, *9*). Third, mitochondria may be synthesized *de novo*, that is by the spontaneous assembly of proteins and lipids secreted by other cell organoids. This suggestion appears to be supported by some electron microscope studies (*1*, *2*).

In a study of the developing retinal cells of the guppy (*Lebistes reticulatus*), Berger (*2*) showed that cytoplasmic membranes form sac-like structures which enclose areas of cytoplasm containing ribosomes and small vesicles derived from the Golgi complex. The resulting structures ("I bodies") initially have a pore which is occluded later. The resulting mitochondrion-like intermediates eventually differentiate into mature organoids. The mitochondriogenesis in special integumentary cells of the larval sardine described in the present paper resembles remarkably the process described by Berger, although we interpret some of our observations slightly differently.

MATERIALS AND METHODS

Larval sardines 4.7–6.1 mm long were fixed in osmium tetroxide buffered at pH 7.4 and embedded in Maraglas. Sections were double-stained in uranyl acetate and lead citrate and observed in an electron microscope (Akashi TRS 50 or E.M. 6B). Photographs were taken at 2000 to 10,000 × and enlarged as required.

ULTRASTRUCTURE OF THE INTEGUMENTARY CELLS IN LARVAL SARDINES

The skin of the larval sardine is a thin epithelium two cells deep (Fig. 1). The outer layer is composed of differentiating scale cells each with a scale anlage. The cells of the inner layer are not so differentiated, although they have much endoplasmic reticulum and appear to be the source of the material which forms the basement membrane of the skin, a structure which we observed to appear gradually as larvae lengthen.

Cells of a third type (here termed special integumentary cells), which resemble the so-called chloride-secretory cells of salmon gills (*8*), appear to be randomly distributed between the upper and lower cell layers of the skin (Fig. 2). These cells are flattened ellipsoids, and are completely covered by scale cells, except for a small area of the apical plasma membrane which abuts on the sea water environment (Fig. 2). In the cytoplasm immediately beneath this free zone, the mitochondria have the structure typical of this organoid, their cristae being of the villous type (Fig. 3). The peripheral cytoplasm, however, is without recognizable mitochondria but does contain structures with a characteristic morphology, hereafter called M bodies (Fig. 4). These M bodies are bound by an inner and outer membrane separated by a space of very varied width. Their matrix contains vacuoles and ribosome-like granules. Using the width of the intermembranous space as a criterion, the M bodies could be divided into three broad groups, which we believe illustrate three main states in the process of mitochondrial formation:

Stage 1

In this group, M bodies have an extreme dilation of the space between inner and outer membranes. These bodies, therefore, often appear as large vacuoles containing a membrane-limited, polymorphic structure (Figs. 5 and 6). Small vacuoles and ribosome-like granules lie in both the matrix of the polymorphic structure and the cytoplasm around it.

Stage 2

These M bodies have an intermembranous space of greatly varied width, although it is often wide at one end of the body (handle) and narrow at the other (head) (Fig. 7). The matrix of the M body, which is enclosed in the inner membrane, is, therefore, often club shaped and contains small tubules with closed ends. These tubules are more numerous in the head than in the handle. As in stage 1, small vacuoles and ribosome-like granules are present in both the matrix and the adjacent cytoplasm (Fig. 7).

Stage 3

This group contains M bodies which have the morphology of the mature mitochondrion of this cell, except for localized regions in which the intermembranous space is still abnormally wide (Figs. 8 and 9).

Despite their differences, the M bodies of all three groups have one common feature which is present in at least some samples of each. At one pole of the body the inner and outer membranes are continuous, the outer membrane turning inward to form the side walls of a narrow, often sinuous, stalk (Fig. 5 and at the arrows in Figs. 6, 7, 9, 10, and 11); through this stalk, the matrix of the M body and the cytoplasm are confluent. The stalk membranes sometimes are broad and diffuse, especially at their proximal end, where the outer membrane turns inward (Figs. 8 and 9). Other stalks have a band of diffuse, moderately electron-dense material running across their proximal ends (Figs. 6, 9, and 11).

Additional features of this cell are vacuoles occurring either singly or in groups (Figs. 3 and 7), and of various sizes. They are usually most conspicuous in the area of cytoplasm in which M bodies are prominent. They may occur, however, anywhere in the cytoplasm, for example, close to the plasma membrane (Fig. 3), or apparently related to the Golgi complex, which has lamellar membranes with localized expansions and many associated small vacuoles and vesicles (Figs. 7 and 12). In addition, they contain a ramifying system of tubular agranular reticulum.

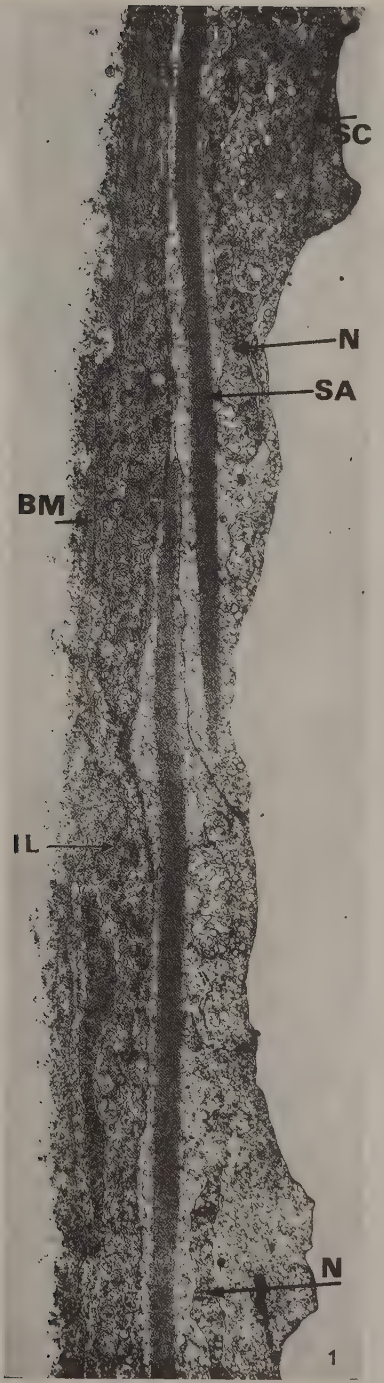
FIG. 1. Area of skin without special integumentary cells. The two cell layers are distinct; the outer layer is of scale cells (*SC*) with scale anlagen (*SA*); the inner layer (*IL*) is without scales and may be responsible for laying down the basement membrane (BM). × 8000.

FIG. 2. Central region of a special integumentary cell which resembles the chloride cell of salmon gills. The scale cells (*SC*) overlap this cell peripherally, but leave a free apex (*AP*, between the arrows) under which are large mitochondria (*M*). The inner epidermal layer underlies the special integumentary cells at *IL*. × 14,250.

FIG. 3. A normal mitochondrion with villous cristae in a special integumentary cell. The cell contains a ramifying tubular system (*TS*). *V*, small vacuoles. × 45,000.

FIG. 4. The peripheral region of a special integumentary cell, showing the large vacuoles and a variety of stages of mitochondriogenesis. *SC*, scale cell; *IL*, inner layer of epidermis. × 12,000.

FIG. 5. Stage 1, early. A cytoplasmic process (*P*) has invaginated a short distance into the vacuole (*V*). × 30,000.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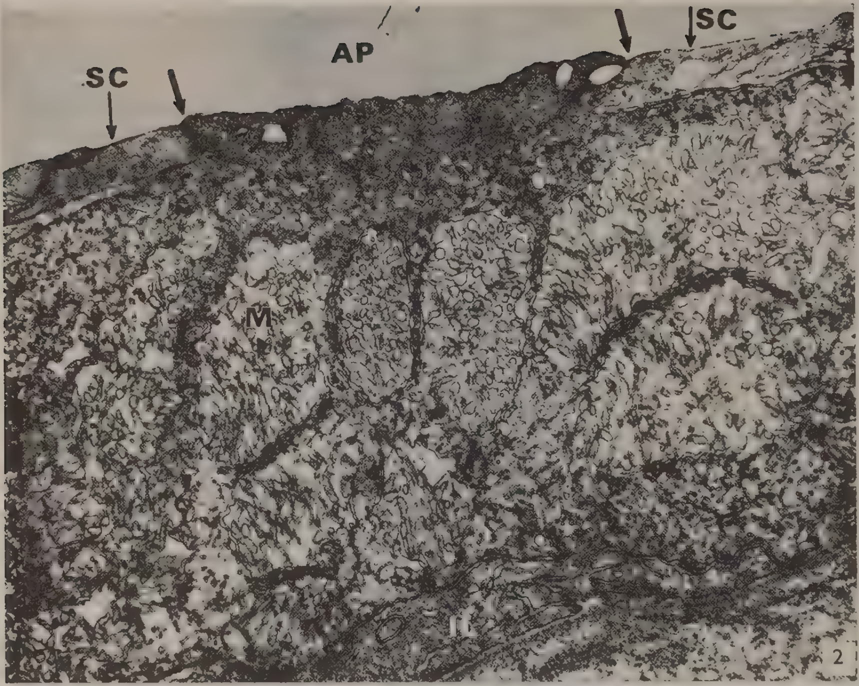

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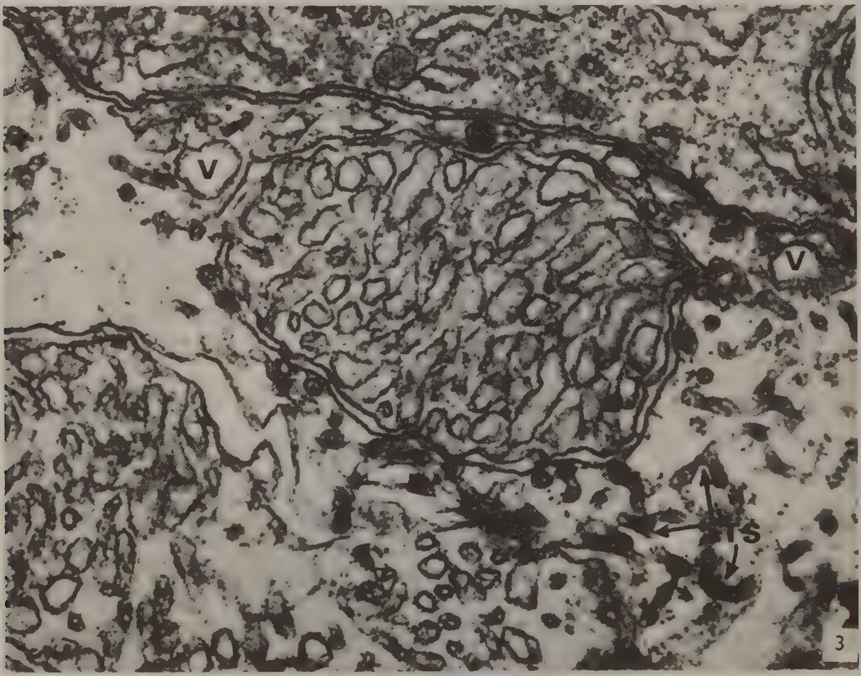

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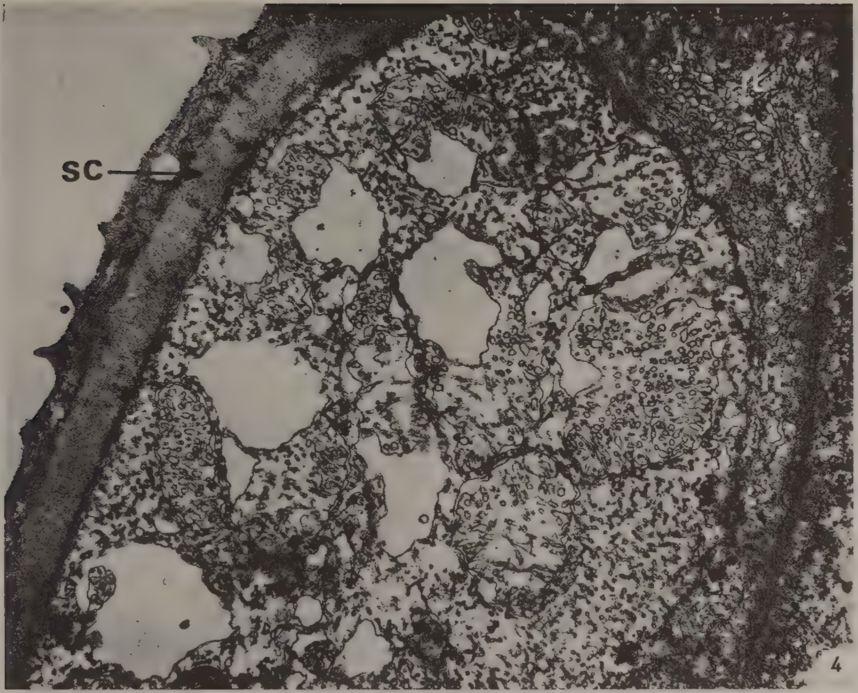

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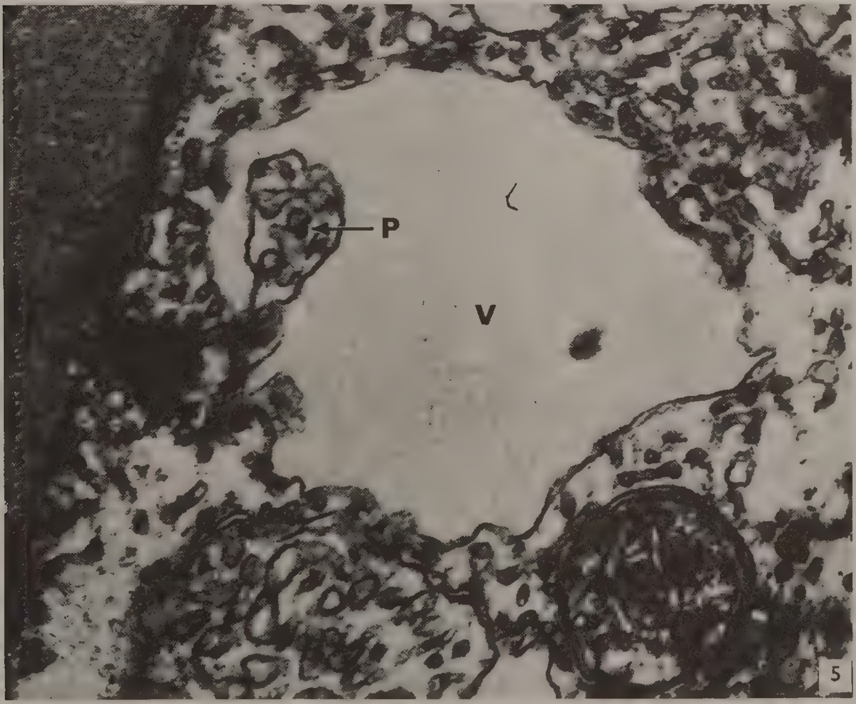

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MITOCHONDRIOGENESIS IN THE SPECIAL INTEGUMENTARY CELL

The unusual morphology of these three groups of M bodies and of the many other intermediate forms, seem to be stages in a process of mitochondriogenesis. We suggest that the process has the following sequence (Fig. 13):

1. Small vacuoles arise in the basal and peripheral cytoplasm.
2. The small vacuoles either grow or fuse together to form a limited number of larger vacuoles.
3. A finger-like invagination of the cytoplasm arises at one pole of a large vacuole and pushes progressively toward the other pole, expanding and carrying in small vesicles and ribosome-like granules as it does so.
4. The invagination gradually fills the vacuole. Simultaneously closed tubules increase in numbers and are initially most numerous at the end distal from the stalk.
5. Finally, the stalk is occluded by the fusion of its walls with those of the vacuole. Subsequently a fully formed mitochondria of normal morphology develops.

The report by Berger (*2*) on work with the retinal cells of the guppy considered that lamellar membranes in the perinuclear region incompletely wrap around cytoplasm containing vesicles derived from the Golgi complex and ribosomes, leaving a small pore. He stated that the resulting "I" bodies (smaller than, but closely resembling, the M bodies of stage 2 described here), eventually develop into mature mitochondria by closure of the pore and the evolution of cristae. This interpretation does not apply completely to mitochondriogenesis in the integument cells of larval sardines because the large vacuoles appear first and are followed later by invaginations which develop stalks. No structures which could be interpreted as stages in the enclosure of cytoplasm, ribosomes, and vesicles by lamellar membranes were observed in this study.

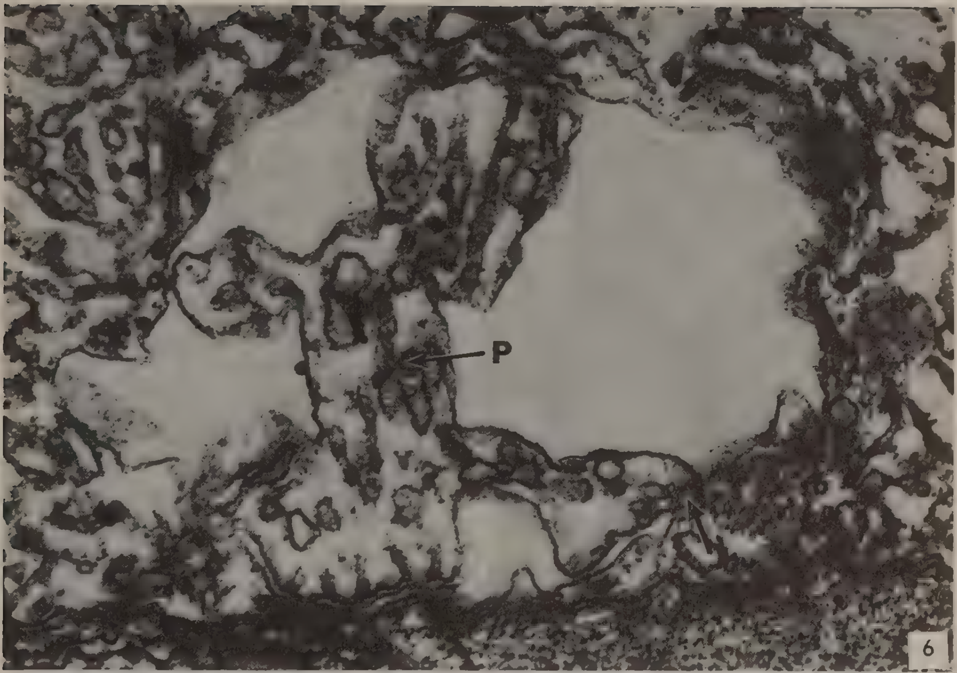
Despite these slight differences in interpretation, however, the observations reported here agree remarkably with those of Berger. The similarities between the two sets of observation are:

1. The peripheral-central gradient of mitochondrogenesis in the special integumentary cell, which is analogous to the vitreal-scleral gradient in the retinal cell.
2. Irregularities of the intermembranous space occurs in both M and I bodies.

FIG. 6. Stage 1, late. A polymorphic cytoplasmic process (*P*) has invaginated into the vacuole. The surrounding cytoplasm and *M* body matrix are continuous at the arrow. ×35,700.

FIG. 7. Stage 2. A club-shaped invagination occupies the vacuole and is attached by a stalk at the arrow. The closed tubules occur in the head of the invagination (at *X*), but only small vacuoles occur in the handle (at *Y*). Note adjacent small vacuoles at *V*. ×22,500.

FIGS. 8 and 9. Stage 3. Two M bodies with the morphology of an almost normal mitochondrion, except for localized zones of extremely wide intermembranous spaces (*IS*). A stalk is evident between the arrows in Fig. 9. Fig. 8, ×32,500; Fig. 9, 32,500.



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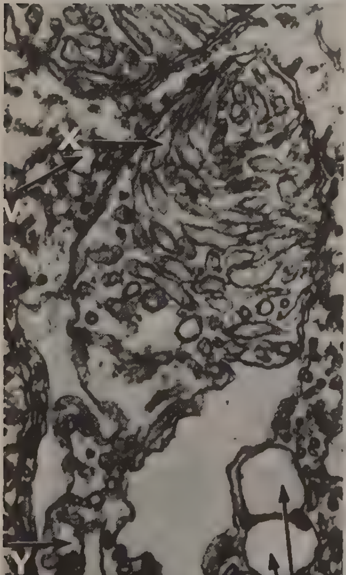

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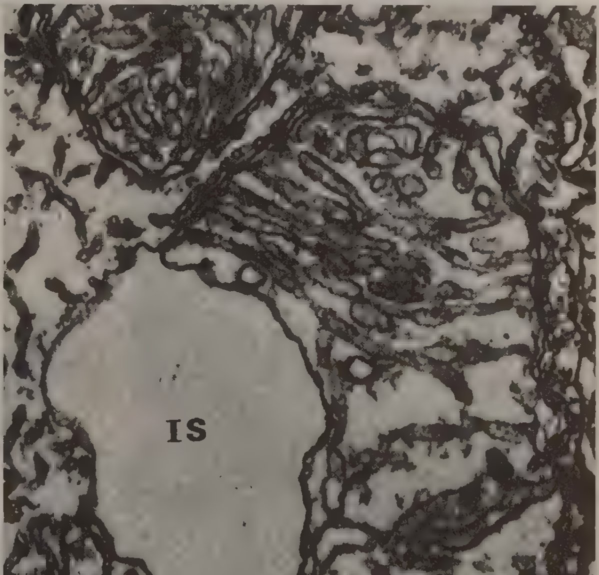

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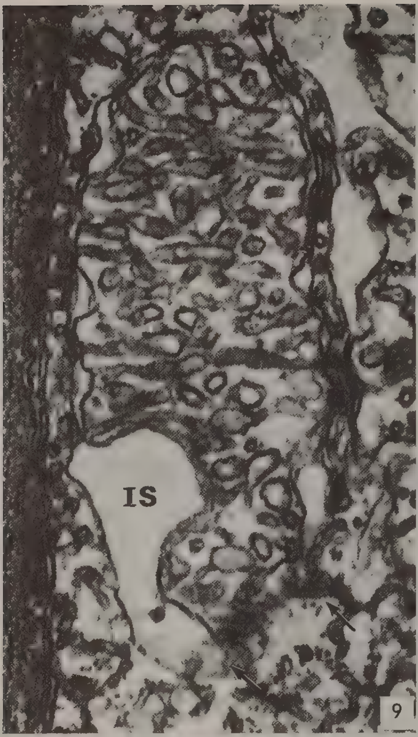

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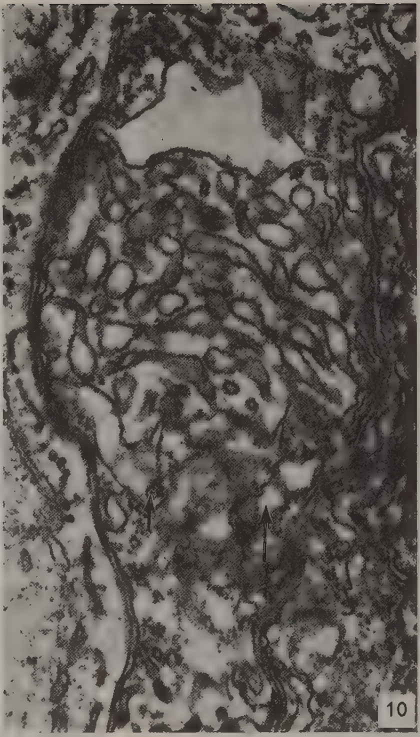

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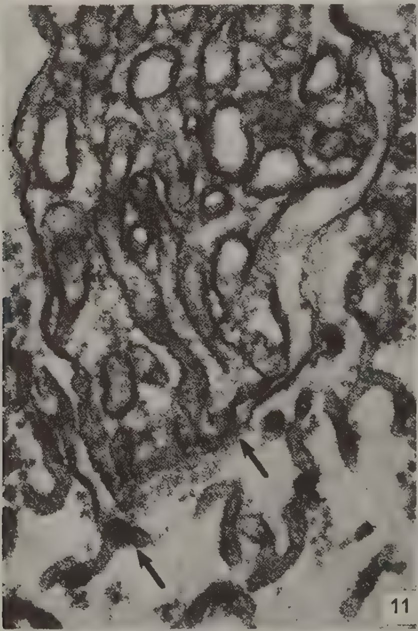

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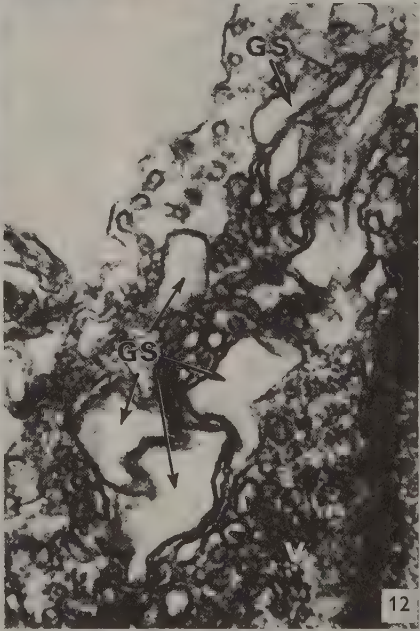

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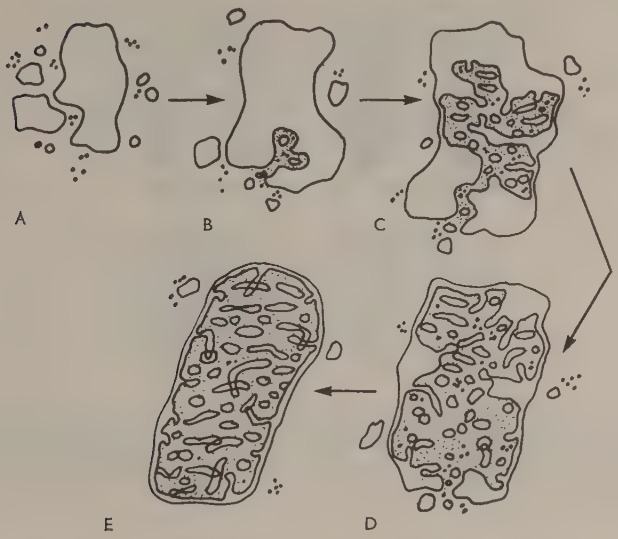

FIG. 13. Schematic representation of mitochondriogenesis in the special integumentary cells of sardine larvae. (A) Vacuoles and vesicles lying free in the cytoplasm. (B) Stage 1. (C) Stage 2. (D) Stage 3. (E) Fully formed mitochondrion with villous cristae.

3. The stalk of the M body, which allows continuity of matrix and cytoplasm, is analogous to the pore of the I body.

4. Vesicles of similar appearance and dimensions occur inside and outside both M and I bodies.

5. The presence of granules, which have the same dimensions as the ribosomes of the surrounding cytoplasm, inside both M and I bodies.

6. The peripheral-central gradient changes in inner membranes (vacuoles to tubules) in the M bodies is analogous to the changes (vesicles to disks) in the I bodies. The connection between inner membrane and cristae appears to be a secondary condition in both types of bodies.

7. The origin of the primordial membranes which give rise to the M and I bodies is unknown. These membranes may arise *de novo* in the cytoplasm or may be partly or wholly derived from existing membranes.

8. Both our observations and those of Berger were made on differentiating cells of larval teleosts.

FIGS. 10 and 11. A stalk connecting the mitochondrial matrix with the cytoplasm is evident between the arrows. Compare Fig. 11 with Fig. 14. Fig. 10, × 33,000; Fig. 11, × 80,000.

FIG. 12. A Golgi complex with swollen Golgi sacs (*GS*) and associated vacuoles and vesicles (*V*). × 36,000.

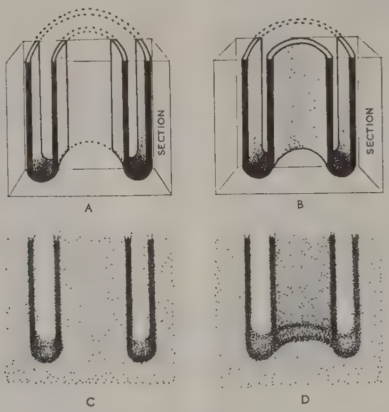

FIG. 14. (A and B) Three dimensional diagrams of sections through the stalk of *M* bodies in either stage 1, 2, or 3. (A) A section cut within the lumen of the stalk; (B) a section which includes part of the wall of the stalk and the curvature where the inner membrane becomes the outer one. (C and D) Diagrammatic representation of photographs of sections such as A and B, respectively.

In the present study the stalk of the M bodies does not always appear clearly. The diffuse band across the base of the stalk and the indefinite appearance of stalk membranes in the same area are due to the sinuous form of the stalk itself. The thickness of most sections includes a portion of the curvature of the stalk wall and the whole region where the base of the stalk fans outward to become the outer membrane. This latter region, when viewed in section from the front, appears as a continuous diffuse band across the base of the stalk due to its curvature (Fig. 14 B and D). Similarly, the outer membrane, because of its curvature at the base of the stalk, is sectioned obliquely and appears broad and indefinite. There is only a remote chance that a section will pass longitudinally through the lumen of the stalk so as to cut opposite walls of the stalk transversely (Fig. 14 A and C).

We thank the Wellcome Trust for a grant to purchase an Akashi TRS 50 electron microscope, the Royal Society for a Reichert Ultramicrotome, and the D.S.I.R. for an E.M. 6B electron microscope. We acknowledge with thanks the technical assistance of Mrs. Gail Theilacker and Mr. A. Lyness.

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Chesapeake Science Vol. 8, No. 2, p. 130–133 June, 1967

Attachment of Hydrofoils to Otter Boards for Taking Surface Samples of Juvenile Fish and Shrimp[1]

ABSTRACT: Regular otter trawl boards were converted to surface trawl boards by attaching hydrofoils to the top edge of the boards. The conversion is simple and inexpensive. The converted otter boards were used to change a bottom trawl into a surface trawl that can be fished from one boat in the same manner as bottom gear. This trawl was efficient in sampling juvenile alewife (*Alosa pseudoharengus*), blueback herring (*A. aestivalis*), and brown shrimp (*Penaeus aztecus*).

Introduction

Few types of towed fishing gear will capture effectively the juvenile fish and shrimp that inhabit surface waters. Types now in use for surface sampling include plankton nets and otter, beam, midwater, and surface trawls. These nets, as presently used, are inadequate or inefficient for accurately estimating the abundance of animals in surface waters.

In general, plankton nets are too small to capture juvenile fish and shrimp effectively. A large plankton net mounted on a sled was used by Chadwick (1964) to sample young striped bass at various water depths. For subsurface samples, the sled was towed at a depth of 5 feet by a short length of towing cable. He stated that striped bass longer than 2.0 inches (fork length) apparently were sampled inefficiently by the gear (larger fish avoided the net).

Otter and beam trawls are sometimes used to capture fish and shrimp at the water surface by towing the net close to the boat so that the float line cannot descend below the surface. Two major disadvantages are apparent with this sampling technique if the resulting data are to be used quantitatively. When the net is so close to the boat, it is difficult to strain constant volumes of water because of currents created by the propeller and by the moving boat. Secondly, one cannot assume that the boat does not frighten some of the animals away from the path of the trawl.

The beam trawl can be converted into one that samples surface waters by attaching hydrofoils or flotation devices to the frame. The beam trawl, as compared with the otter or midwater trawl, however, is cumbersome and creates more surface turbulence while it is towed. Massmann, Ladd, and McCutcheon (1952) converted an otter trawl into a surface trawl, but had to use two boats to pull the net. The net was, nevertheless, efficient in sampling clupeoid fishes in Virginia. Lavenberg and Fitch (1966) used a midwater trawl towed at high speed to take surface samples in the Gulf of California but they did not mention its efficiency in relation to tows made at other depths.

Description of Gear

A 10-foot and an 18-foot otter trawl, similar to those described by Bullis (1951), were modified by attaching hydrofoils to the top edge of the otter boards. These hydrofoils kept the trawl boards at, or just under, the water surface as they were being towed (Fig. 1). Dimensions of the otter board and hydrofoil for the 10-foot trawl are shown in Figure 2. A brass runner was attached to the front and bottom edges of the otter board for connection of the hydrofoil, and for balance.

The hydrofoil is adjustable so that various angles between the upper edge of the otter board and lower surface of the hydrofoil can be formed. A 30° angle, used on the board described, caused the anterior end of the hydrofoil to run just below the water surface when the trawl was towed at various distances behind the boat. Lengths and the spacing of the points of attachment of the bridle chains to the board were based on ratios given by Bullis (1951). Each otter board, including hydrofoil and bridle chains, weighed about 14 pounds.

Sampling Advantages of the Surface Trawl

Otter trawls converted into surface trawls were effective in capturing juvenile alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in Albemarle Sound, North Carolina, and juvenile brown shrimp (*Penaeus aztecus*) in Boli-

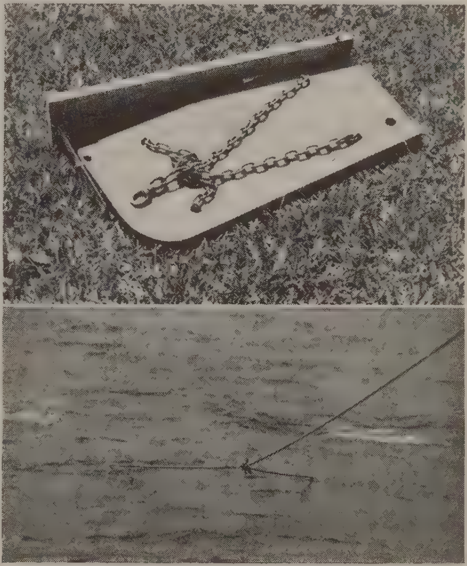

Fig. 1. Otter board converted for surface trawling and the trawl being towed.

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[1] Contribution No. 225, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

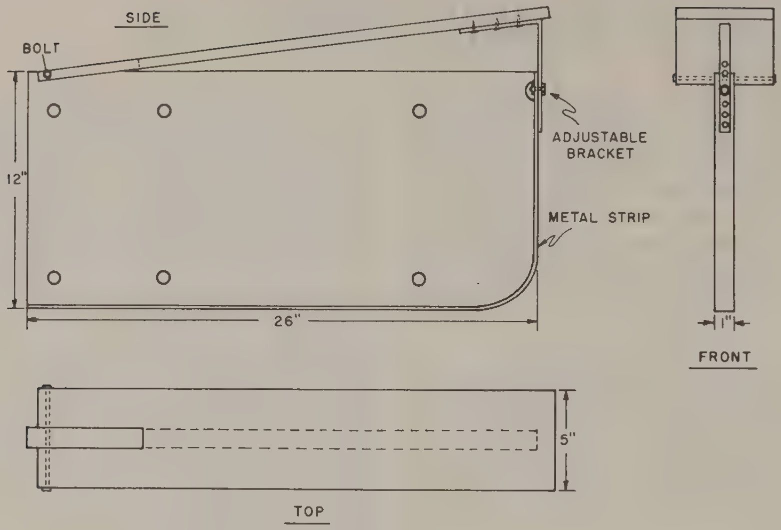

Fig. 2. Method of attachment of hydrofoil to otter board.

var Roads, Texas (tidal pass between Galveston Bay and the Gulf of Mexico). Catch per unit of effort by the surface trawl was often 20 times as great for herring and 5 times for shrimp as alternate bottom tows with the same size of trawl.

Catches with the surface trawl in Bolivar Roads often contained shrimp only. These shrimp were in better condition than those taken with the bottom gear. Thus, the surface trawl, on occasion, can be used efficiently in obtaining shrimp for marking studies.

The surface trawl has many advantages over other types of fishing gear for taking surface samples of fish and shrimp. It can be made easily as bottom trawls presently available at most estuarine research stations can be converted quickly and inexpensively. Thus, the surface trawl can be used to estimate relative abundance of surface-dwelling animals which bottom trawls rarely capture.

Within limits any size of trawl can be used. This conversion reduces greatly the problem of escapement of larger animals from plankton nets that are used for surface sampling. The surface trawl can be fished as easily as a bottom trawl. A regular, or converted, otter trawl is less expensive and easier to handle than a similar size of beam trawl.

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Size of Brown Shrimp and Time of Emigration from the Galveston Bay System, Texas[1]

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Abstract

A study was begun to determine the time period of emigration, the vertical distribution, and the size of juvenile and subadult brown shrimp leaving the Galveston Bay system, Texas, through the Bolivar Roads tidal pass to the Gulf of Mexico. The sampling gear consisted of a bottom and a surface trawl. Samples were taken both day and night on ebbing tides from May 18 to August 1, 1966.

Brown shrimp were caught throughout the sampling period. Two peaks occurred, the first in May and the second in June. Estimates of mean catch per unit of effort indicated that the shrimp were near the surface at night and near the bottom during the day.

The mean lengths of brown shrimp taken during the day and night with bottom and surface trawls on the same sampling date were similar. The size of the emigrating shrimp increased significantly as the season progressed.

INTRODUCTION

MANY ANIMALS spend part of their lives in estuaries. Adult brown shrimp (*Penaeus aztecus*), which contribute to the Texas commercial fishery, spawn offshore in the Gulf of Mexico. Postlarvae (8 to 14 mm total length) move into the estuaries, grow for about 2 months and leave as juveniles and subadults (60 to 130 mm total length). It is important to develop accurate sampling procedures for estimating the size, relative abundance, and time of emigration of shrimp from estuaries to gain a clear understanding of the life histories.

Objectives of this study are to determine for juvenile and subadult brown shrimp: (1) the peaks of emigration; (2) the size at which they leave the Galveston Bay system; and (3) whether size or catch per unit of effort varies between surface and bottom, or between day and night. A further objective was to provide data essential for designing a more efficient sampling system for obtaining information on the preceding points.

Copeland (1965) used a tide trap set at mid-depth to sample animals moving with the tides in Aransas Pass Inlet, Texas. He collected brown shrimp during ebb tides from March 10 to December 31, 1963. Peaks of abundance usually occurred during full moon in May, June, July, and

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August. He stated (data are not shown) that the timing of peaks of emigration were similar during the summer of 1964. The emigration of pink shrimp (*P. duorarum*) resembled that of the brown shrimp except that they were caught only during April through September. He concluded that apparently the high tides and faster currents that accompany the time of full moon were enough to stimulate the movement of these shrimp from the bay nursery grounds.

Copeland (1965) stated that juvenile and subadult shrimp emigrated through the Aransas Pass Inlet at about the same size regardless of whether the time was May or June. On the basis of small numbers caught, he also stated that length frequencies were similar through September. Most of the brown shrimp emigrants were between 70 and 80 mm total length whereas most of the pink shrimp emigrants were between 70 and 90 mm.

Idyll (1963) and Idyll, Iversen, and Yokel (1964) used a channel net that blocked the entire 60-foot width of Buttonwood Canal in Everglades National Park near Flamingo, Florida, to catch juvenile pink shrimp moving on ebb tides from adjacent estuarine areas. Idyll, et al. (1964) stated that two of the more important sources of catch variation are speed of ebbing current and phase of the moon. In months when samples were taken in ebb currents during or near the new and full moon, the numbers of shrimp were consistently higher than during other moon phases. Also, numbers of shrimp taken decreased abruptly just after dawn and no shrimp were caught in full daylight.

Idyll (1963) observed that for pink shrimp (1) the mode and size range were identical for 5 months, December 1962 through April 1963; (2) distributions shifted markedly to the right beginning in early May and continuing through June; and (3) average size decreased because of the disappearance of large shrimp and the appearance in catches of a new group of smaller shrimp after June.

Beardsley and Iversen (1966) determined the vertical and horizontal distribution of juvenile pink shrimp as they moved out of the nursery grounds through Buttonwood Canal, Florida. The sampling gear consisted of 13 conical nets suspended in the canal on 5 iron frames. Sampling was at night during ebb tides on full moon, new moon, and quarter moon. On the average, the percentage of the shrimp caught at or near the surface was about 91% during full moon but only about 75% during new and quarter moon. Lateral distribution varied significantly in the surface layers.

AREA AND SAMPLING PROCEDURE

The Galveston Bay system in southeast Texas exchanges water with the Gulf of Mexico through three passes (Fig. 1A and 1B). About 85% of this exchange is through Bolivar Roads (U.S. Army Corps of Engineers, personal communication). The Bolivar Roads tidal pass was, therefore, chosen for sampling brown shrimp as they moved from the Galveston Bay system to the Gulf of Mexico.

Samples of brown shrimp were taken at station 1 in the tidal pass and at station 2 just outside the jetties in the Gulf of Mexico (Fig. 1C). Water depths (mean low tide) at stations 1 and 2 were about 26 and 32 feet, respectively. I assumed that samples taken at station 1 represented shrimp emigrating from the bay system. Reasons for this assumption are: (1) station 1, if the jetties are ignored, would be in the Gulf of Mexico; (2) shrimp taken at station 1, as compared to those taken in the Galveston Bay system on similar dates, averaged larger and showed less variation in length; and (3) station 1 does not resemble the habitats preferred by shrimp in the bay system. Samples were taken at station 2 to compare the size of shrimp in the Gulf of Mexico with the size of those from the tidal pass.

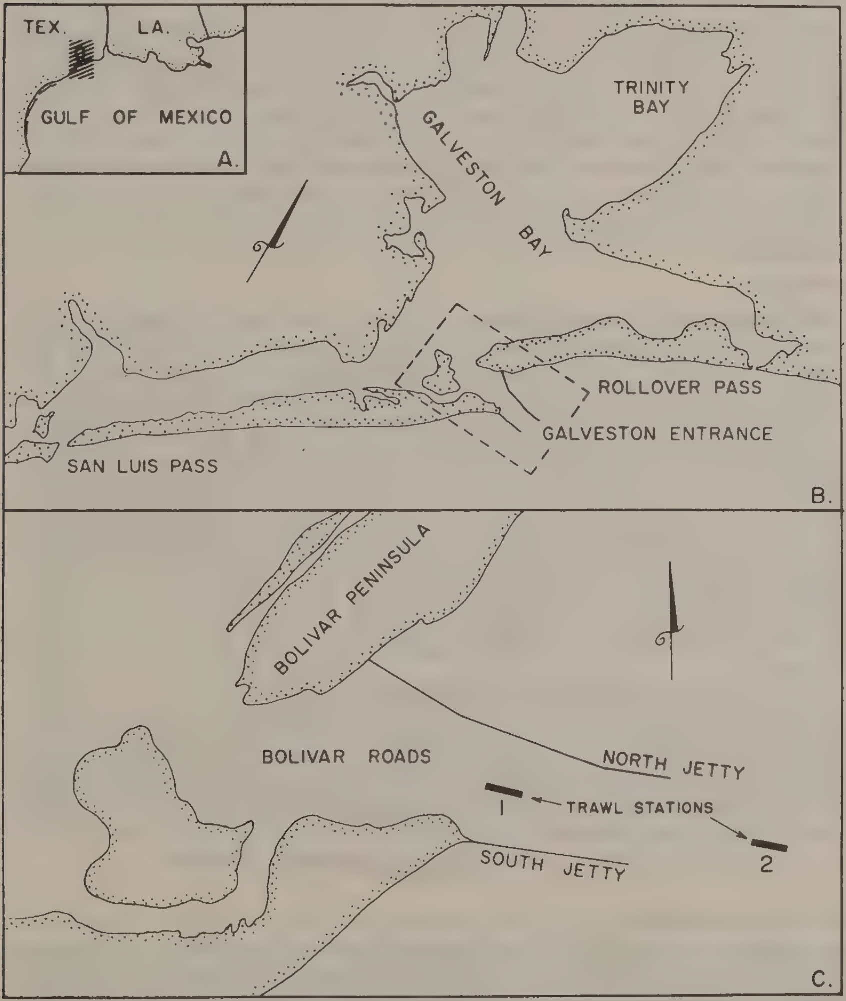
TEX.
LA.
GULF OF MEXICO
A.
GALVESTON BAY
TRINITY BAY
ROLLOVER PASS
GALVESTON ENTRANCE
SAN LUIS PASS
B.
BOLIVAR PENINSULA
BOLIVAR ROADS
NORTH JETTY
1
TRAWL STATIONS
2
SOUTH JETTY
C.

Fig. 1. The Galveston Bay system and Bolivar Roads tidal pass showing locations of station at which trawl samples were taken.

Samples used to estimate abundance and the size at emigration were taken, usually at 4-day intervals, from May 18 to August 1, 1966, with an otter trawl that had an opening of 2 x 10 feet. The cotton webbing had stretched mesh of 1.5 inches in the body and 1.1 inches in the cod end. Bottom and surface samples were taken by using regular and converted otter boards, respectively. Occasional mid-water tows were made with the bottom trawl by letting out only a short length of towing cable. A few samples were taken during flood tides. Shrimp caught in the mid-water tows or on flood tides were not used in the analyses of catch per unit of effort.

Most of the samples were taken by towing the trawl 8 minutes against the ebbing tides from the 40-foot vessel TOMMY BOX at an engine speed of 900 r.p.m. Samples were taken both day and night, usually within 2 hours of maximum ebb tide as predicted by the U.S. Coast and Geodetic Tide Tables (1966). I observed the direction of water flow past a buoy adjacent to station 1 to insure that the samples were collected during ebbing tides.

Total length (tip of rostrum to tip of telson) of all brown shrimp caught was measured to the nearest millimeter immediately after capture.

Abundance

Summary statistics for the analyses of catch per unit of effort (Tables 1 and 2) indicate that the mean number of brown shrimp caught per minute (efficiency) at station 1 was greatest on the bottom during the day and greatest at the surface at night. Catch-per-minute data used to compute the weighted means shown in the last row of Table 2 were compared by analysis of variance (Steel and Torrie, 1960: 134). A significant difference was not found ($F=1.66$; $F_{.10}=2.49$ for 2 and 15 d.f.). I think, however, that the difference in the estimates of mean catch per minute shown in the bottom line of Table 2 are real, but the high variability and the small number of sampling dates available for comparison made it impossible to support the view statistically. If the differences are real, the relative efficiencies shown in the bottom line of Table 2 indicate that the shrimp were near the surface at night and near the bottom during the day.

All data shown in Table 1 were combined by date to estimate the relative abundance of brown shrimp as they emigrated through the tidal pass (Table 2 and Fig. 2). I assume that Fig. 2 accurately depicts the two major peaks of emigration during the sampling period, the first in mid-May and the second in mid-June. Brown shrimp were leaving the bay system when I started sampling (May 18). Thus, the magnitude of the first peak and the timing of emigration in May are unknown.

Size at Emigration

The mean lengths of brown shrimp taken during the day and night with bottom and surface trawls on the same sampling date were similar (Table 3). Mean lengths of brown shrimp taken in the tidal pass and in the Gulf of Mexico on a given sampling date were similar also. On May 18, the mean length of 190 shrimp from station 1 was 58.0 mm and the length for 40 shrimp from station 2 was 62.0 mm. On May 30, 226 shrimp

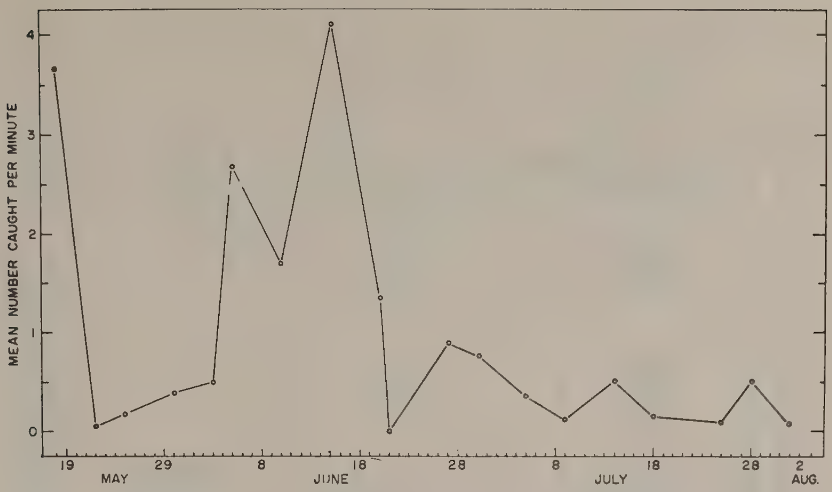

Fig. 2. Catch of brown shrimp per trawling minute as they emigrated through the Bolivar Roads tidal pass.

caught at station 1 on both ebb and flood tides had a mean length of 81.7 mm and 222 shrimp from station 2 had a mean length of 76.6 mm.

All shrimp caught at station 1 were combined by weekly intervals to represent the size of emigrating brown shrimp during the study (Fig. 3). In addition to the shrimp used in the catch-per-unit-of-effort analyses (Table 1), the graph in Fig. 3 includes 402 shrimp taken during flood tides and 129 taken with a mid-water trawl at station 2 (27 shrimp were discarded because they were too mutilated to measure).

Brown shrimp caught from May 14 to 21 had a mean length of 58.0 mm (Fig 3). Mean length was much greater (79.7 mm) the following week (May 22 to 28) and then the mean lengths tended to increase gradually for the remainder of the sampling period. The weekly length frequencies approximated normal distributions.

A linear relation between mean length and the time at emigration of brown shrimp is shown in Fig. 4. The null hypothesis that the regression coefficient ($b = 3.61$) was equal to zero was tested to determine if the mean sizes were similar at different times. The hypothesis was rejected ($t = 9.02$; $t_{.01} = 3.17$ for 10 d.f.). I concluded that size at emigration increased significantly during the study.

SUMMARY

Peaks in abundance of brown shrimp emigrating from the Galveston Bay system occurred in May and June 1966. The mean number of brown shrimp caught per minute was greatest on the bottom during the day and greatest at the surface at night. The mean lengths of brown shrimp taken during the day and night with bottom and surface trawls on the same sampling date were similar. The size of the emigrating shrimp increased significantly as the season progressed.

TABLE 1

NUMBER OF TOWS, TOWING TIME, AND NUMBER OF BROWN SHRIMP CAUGHT IN TRAWL SAMPLES TAKEN ON EBBING TIDES AT STATION 1 IN THE TIDAL PASS

	Surface						Bottom					
	Day			Night			Day			Night		
Date (1966)	Number of tows	Number trawling minutes	Number shrimp caught	Number of tows	Number trawling minutes	Number shrimp caught	Number of tows	Number trawling minutes	Number shrimp caught	Number of tows	Number trawling minutes	Number shrimp caught
May												
18							3	25	118	4	30	83
22										3	20	1
25										3	25	4
30							4	32	13			
June												
3										5	40	20
5							2	11	29			
10							7	56	94			
15							10	80	327			
20	1	8	0	4	32	146	13	104	92	5	40	9
21				3	24	0				2	16	0
27	4	32	0	6	44	1	3	24	105	2	16	1
30	4	32	0	12	80	134	12	96	47	2	16	3
July												
5				8	64	23						
9	2	12	0							6	44	15
14	1	8	0	6	48	39	2	16	3	2	16	4
18	3	24	1	8	64	14	4	32	3	3	24	7
25	1	8	0				9	72	8			
28	1	8	0	4	36	33	3	24	3	1	8	2
August												
1				5	40	5				5	40	1
Totals	17	132	1	56	432	395	72	572	842	43	335	150

TABLE 2

THE MEAN NUMBER OF BROWN SHRIMP CAUGHT PER MINUTE IN TRAWL SAMPLES TAKEN ON EBBING TIDES AT STATION 1 IN THE TIDAL PASS

	Surface		Bottom		
Date (1966)	Day	Night	Day	Night	All data combined
May					
18			4.72	2.77	3.65
22				0.05	0.05
25				0.16	0.16
30			0.41		0.41
June					
3				0.50	0.50
5			2.64		2.64
10			1.68		1.68
15			4.09		4.09
20[1]	0.00	4.56	0.88	0.22	1.34
21		0.00		0.00	0.00
27[1]	0.00	0.02	4.37	0.06	0.92
30[1]	0.00	1.67	0.49	0.19	0.82
July					
5		0.36			0.36
9	0.00			0.34	0.27
14[1]	0.00	0.81	0.19	0.25	0.52
18[1]	0.04	0.22	0.09	0.29	0.17
25	0.00		0.11		0.10
28[1]	0.00	0.92	0.12	0.25	0.50
August					
1		0.12		0.02	0.07
Weighted mean — all samples	0.01	0.91	1.47	0.45	
Weighted mean — selected samples	0.01	1.21	0.85	0.22	

[1] Selected samples

TABLE 3

MEAN LENGTH (MILLIMETERS) OF BROWN SHRIMP CAUGHT AT STATION 1 ON EBB TIDES DURING THE DAY AND NIGHT AND AT THE SURFACE AND ON THE BOTTOM

Date (1966)	Day		Night		Difference	Surface		Bottom		Difference
	Number of shrimp	Mean length	Number of shrimp	Mean length		Number of shrimp	Mean length	Number of shrimp	Mean length	
May 18	109	58.5	81	57.5	+1.0					
July 20	92	89.1	150	80.5	+8.6	96	88.8	146	80.5	+ 8.3
27	105	90.8	2	84.5	+6.3					
30	47	90.0	137	92.3	—2.3	50	89.2	134	92.7	— 3.5
July 14	3	95.2	42	99.7	—4.5	7	92.4	39	100.5	— 8.1
18	3	99.3	21	99.6	—0.3	10	104.6	15	96.2	+ 8.4
28	3	103.6	33	108.4	—4.8	5	97.2	33	109.4	—12.2

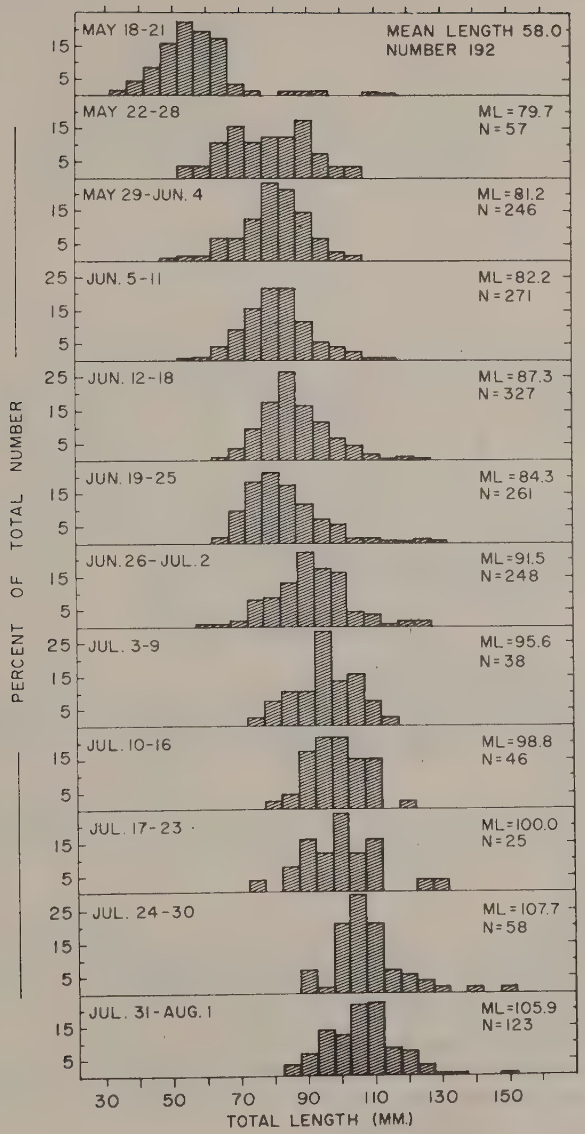

Fig. 3. Length-frequency distributions by week of brown shrimp caught in the Bolivar Roads tidal pass.

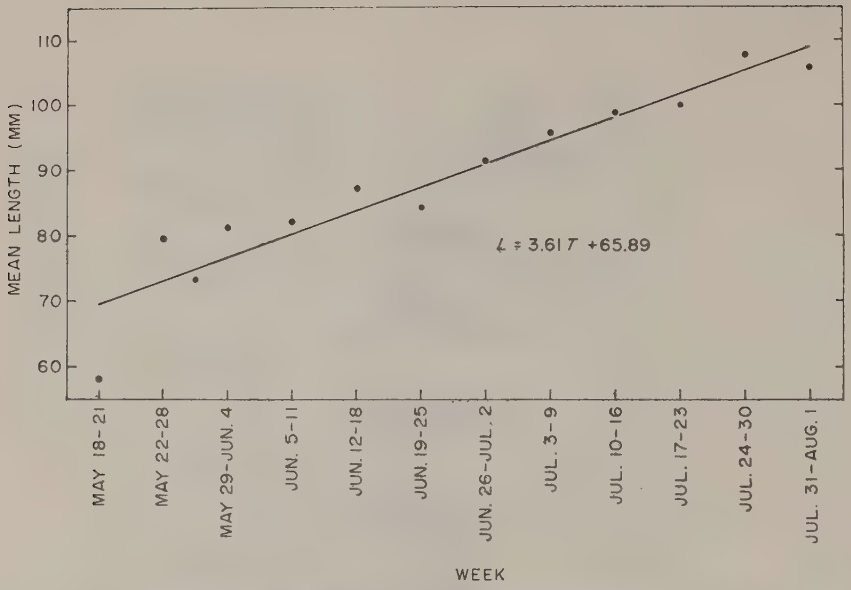

Fig. 4. Increase in mean length of brown shrimp caught in the Bolivar Roads tidal pass, May 18-August 1966.

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Bacteria have been shown to be etiological agents in the pathology of larval bivalve mollusks. Although histological evidence indicates the probability of bacterial disease in adult oysters, experimental infection has not been achieved. Because of immediate, prolonged adduction of their tightly-closing valves, attempts to introduce infectious material into oysters (or hard clams) usually involve force and trauma. The soft-shell clam, *Mya arenaria*, is unable to seal its valves and relaxes readily, exposing soft tissue and a large siphon. This species is free from fouling organisms and is readily available at all seasons in New England and mid-Atlantic areas. Suspensions of the five strains of *Vibrio* sp. that cause bacillary necrosis in larval bivalves were injected into the heart, siphon tissue, and the incurrent and excurrent siphon lumina of soft-shell clams. All strains of the vibrio caused significant mortality; most deaths occurred within 2 days. Heaviest losses resulted from heart and excurrent siphon injections. No mortality occurred in controls injected with seawater, broth, *Serratia* sp., and *Escherichia coli*. The soft-shell clam appears to be a valuable animal for testing the pathogenicity of marine microorganisms for bivalve mollusks.

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Occurrence of the Parasitic Isopod *Olencira praegustator* in the Yellowfin Menhaden, *Brevoortia smithi*

Olencira praegustator, a parasitic cymothoid isopod, was described by Latrobe (1802) from Atlantic menhaden, *Brevoortia tyrannus*, captured in the York River, Virginia. Goode (1879) and Ellison (1951) reported a high incidence of this apparently genus-specific parasite in *B. tyrannus* along the southeastern seaboard. Goode (1884) and Richardson (1905) recorded it from the Gulf menhaden, *B. patronus*, a cognate species in the Gulf of Mexico. To our knowledge, however, the occurrence of this parasite has not been documented in the finescale menhaden, *B. gunteri*, or the yellowfin menhaden, *B. smithi*, (Gunter and Christmas, 1960; Hildebrand, 1963).

In March 1965, gill nets fished from the Bureau of Commercial Fisheries R/V *George M. Bowers* caught 101 yellowfin menhaden in St. Joseph Bay, Apalachicola Bay, St. George Sound, and in the Gulf of Mexico off St. George Island, Florida (Figure 1). Of these fish, 66 were parasitized with *O. praegustator* (Table 1).

Most of the parasitized fish contained a single large isopod firmly attached to the gill arches by the dactyli of the last pair of legs and to the roof of the front part of the mouth by the dactyli of the smaller anterior legs (Figure 2); a few fish also contained a small isopod attached to the gill filaments. The rear

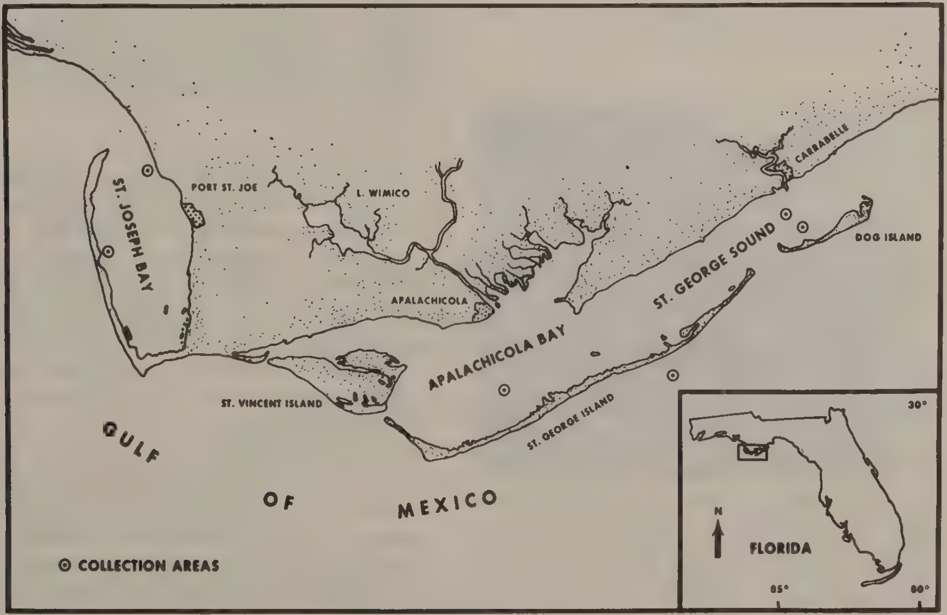
PORT ST. JOE
L. WIMICO
ST. JOSEPH BAY
CARRABELLE
DOG ISLAND
ST. GEORGE SOUND
APALACHICOLA
APALACHICOLA BAY
ST. VINCENT ISLAND
ST. GEORGE ISLAND
GULF
OF
MEXICO
⊙ COLLECTION AREAS
30°
N
FLORIDA
85°
80°

FIGURE 1.—Collection locations of yellowfin menhaden in March 1965 during Cruise 58 of the R/V *George M. Bowers*

TABLE 1.—*Physical data from Cruise 58 of the R/V* George M. Bowers *and incidence of* Olencira praegustator *in the yellowfin menhaden*

Date March 1965	Locality		Surface tempera-ture C	Number of yellowfin menhaden	Number in-fested
	North latitude	West longtiude			
18	29° 48′	85° 25′	17.8	1	1
19	29° 39′	84° 59′	18.3	11	4
19	29° 40′	84° 47′	16.1	50	31
19	29° 48′	84° 39′	18.3	2	2
20	29° 49′	84° 40′	18.3	34	26
21	29° 51′	85° 20′	16.7	3	2

portion of the large parasite's body assumed a lateral position in the branchial chamber, but the front part was oriented upside down in the oral cavity, giving the parasite a twisted aspect in the host. The fourth, fifth, and sixth pairs of legs, often attached to various sections of the gills, furnished additional support. The isopod occupied most of the oral and branchial cavities, but no external deformation of the mouth, such as that reported by Hildebrand (1963), was discernible. Some of the fishes had suffered a small amount of gill-filament erosion, but the condition of the host did not seem to be affected.

The large isopods were 32 to 43 mm long and 9 to 13 mm across the penultimate (6th and widest) thoracic segment; many were gravid. The small isopods were 7 to 9 mm long and 2 to 3 mm wide (Figure 3).

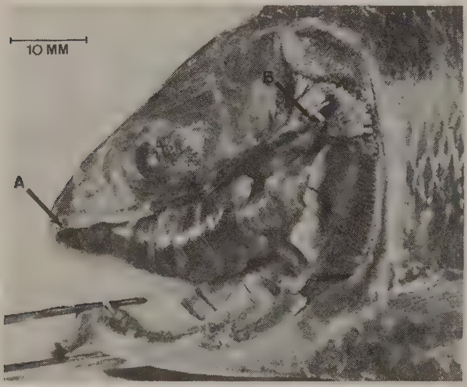

FIGURE 2.—Head of 183-mm yellowfin menhaden with left side of jaws and operculum removed to show position of *Olencira praegustator* in oral and branchial chambers. Arrow A points to head of a 41-mm female isopod and Arrow B to the head of a 7-mm male isopod.

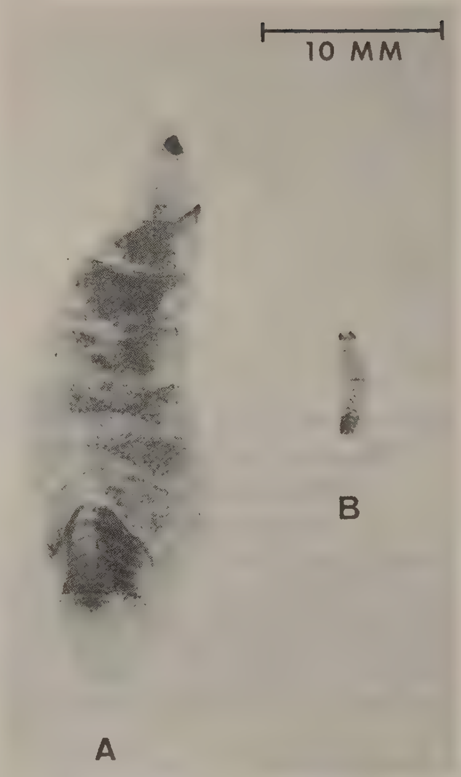

FIGURE 3.—A. Dorsal view of 32-mm female isopod killed in situ and removed from the host. The body distortion conforms to the twisted position of the parasite in the host. B. 7-mm male *Olencira* from the same host.

According to Cheng (1964), cymothoids are sexually dimorphic, the males resembling the young; protandrous hermaphrodites are known among certain genera. The solitary small isopod that occurred in some specimens was surmised to be a male, since young would probably have been present in greater numbers. Whether or not the isopods were protandrous hermaphrodites was not determined.

Parasitism apparently did not vary with size of the fish. Fork lengths of infested fish ranged from 171 to 210 mm, and of uninfested fish from 165 to 210 mm.

Although 770 Gulf menhaden were collected concurrently with the yellowfin menhaden, none harbored the isopod. Possibly these 2 species of fish were segregated when infestation occurred. During the two preceding 1965 months, January and February, 552 non-infested Gulf menhaden, but no yellowfin menhaden, were captured in the same areas. It is also possible that the host-parasite relationship is conspecific rather than congeneric, and closely related but still undescribed *Olencira* are associated with each species of menhaden.

ACKNOWLEDGMENT

We are grateful to Dr. Thomas E. Bowman of the U. S. National Museum for verifying the identity of this isopod.

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Histriobdella homari (Annelida: Polychaeta) in the American Lobster, *Homarus americanus*

A survey of the parasites and commensals of the American lobster (*Homarus americanus* Milne-Edwards, 1837) was begun in 1965 as part of a Bureau of Commercial Fisheries study of the biology and economics of this valuable marine resource.

The rarely reported commensal polychaete, *Histriobdella homari* Van Beneden, 1858 (Fig.

1), is a common associate of American lobsters. Although it has not been previously recognized in American hosts, its widespread distribution in New England waters (Table I) indicates that it is well established in the benthic community of the western Atlantic.

H. homari was originally described from the external egg masses of the European lobster, *Homarus vulgaris,* and the Norway lobster, *Nephrops norvegicus.* It is a monotype and the sole marine representative of the family Histriobdellidae, which contains in addition four species of *Stratiodrilus* whose members occur in the branchial chambers of freshwater crayfishes: *S. tasmanicus* Haswell, 1900 in *Astacopsis tasmanicus* of Tasmania; *S. novae-hollandiae* Haswell, 1914 in *Astacopsis serratus* of Australia; *S. platensis* Cordero, 1927 in *Aeglaea laevis* of Argentina and Chile; *S. haswelli* Harrison, 1928 in *Astacoides madagascariensis* of Madagascar.

Like *Stratiodrilus, Histriobdella* is normally an inhabitant of the branchial chamber and gills of its host. Being small, colorless, and strongly thigmotactic, *Histriobdella* is difficult to detect in life, whether on fragments of egg clusters or on dissected elements of the gills. Once seen, however, *Histriobdella's* remarkable manner of walking and its tenacity are immediately diagnostic. An almost ludicrous but sure progress over the substrate is accomplished by alternate placement of the feet of the posterior limbs; this ambulation is performed in a nearly horizontal plane, with only occasional use of the anterior limbs. The foot of each limb is provided with accessory cement glands which give *Histriobdella* almost complete security with every step.

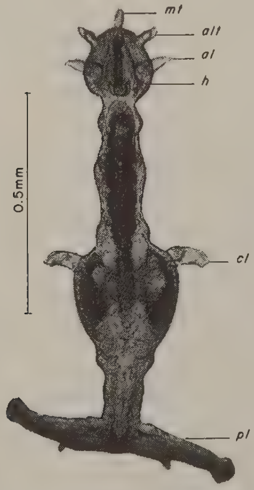

FIGURE 1. *Histriobdella homari.* Photomicrograph of living male with claspers extended. Legend: *al,* anterior limb; *alt,* anterolateral tentacles; *cl,* clasper; *h,* head; *mt,* median tentacle; *pl,* posterior limb.

TABLE I. *Occurrence of* Histriobdella homari *in lobsters from seven New England localities.*

Locality[1]	Sample size	Per cent infected	Mean no. of *Histriobdella* in infected lobsters
Cutler, Maine	10	100	17
Southwest Harbor, Maine	10	100	30
Monhegan Island, Maine	10	100	61
Boothbay Harbor, Maine	110	91	10
Portsmouth, N. H.	10	100	22
Milford, Conn.	8	37	25
Georges Bank	18	61	12

[1] Collections at the first six localities listed were from coastal trap fisheries at depths less than 20 fathoms; at Georges Bank they were from ocean trawls fished at 63 to 100 fathoms.

Shearer's (1910, Quar. J. Micr. Sci. **55**) observations that *Histriobdella* is markedly sensitive to changes in environment suggested a simple isolation technique that has proved efficient in survey work. The lobster gills are removed, submerged in 50% seawater in specimen bowls, and refrigerated overnight; the gills are then discarded and the bottom accumulations are examined with a dissecting microscope. *Histriobdella,* when present, are usually moribund, relaxed, somewhat opaque, and easily detected and counted. Doubtless, some specimens do not work free of the gills, but the technique is satisfactory for estimating frequency of occurrence in samples and for obtaining specimens.

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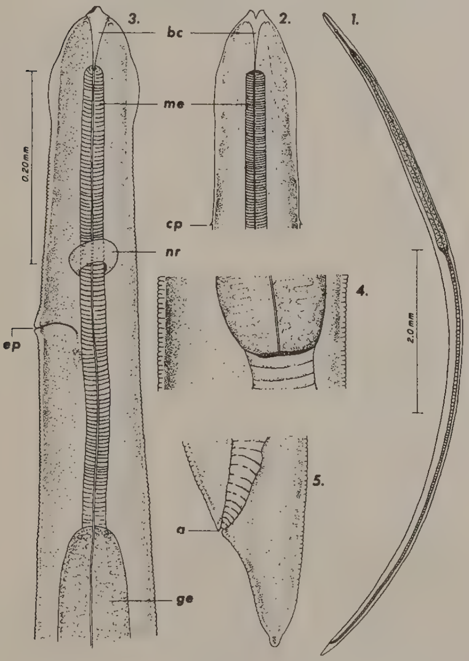
Juvenile *Ascarophis* (Nematoda: Spiruroidea) in the American Lobster, *Homarus americanus*

Adult members of the genus *Ascarophis* Van Beneden, 1871, parasitize the digestive tract of a variety of fishes ranging from Arctic to Antarctic seas. The generalized life cycle of *Ascarophis* was deduced by Uspenskaya (1953, Zool. Zhurnal **32:** 828–832) who related two species of juvenile *Ascarophis* from Barents Sea decapods to adult *A. morrhuae* Van Beneden, 1871, and *A. filiformis* Poljansky, 1952, in the gadoid fishes, *Gadus morhua* L. and *Melanogrammus aeglefinus* (L.).



Figures 1–5. *Ascarophis* sp. juvenile, camera lucida drawings. **1.** Entire worm in lateral view. **2.** Dorsal view of anterior end to level of cephalic papillae. **3.** Lateral view of anterior end to beginning of glandular esophagus. **4.** Lateral view in region of esophagointestinal valve. **5.** Lateral view of tail. Scale line of Figure 3 applies to Figures 2–5. Abbreviations: bc, buccal capsule; me, muscular esophagus; cp, cervical papilla; nr, nerve ring; ep, excretory pore; a, anus; ge, glandular esophagus.

This report documents a third species of juvenile *Ascarophis*, of unknown adult affinities, that occurs in offshore populations of the decapod, *Homarus americanus*. The lobsters were collected in April, June, August, October, and November, 1965 during research cruises along the edge of the continental shelf south and southwest of Georges Bank (off Cape Cod, USA) at 55 to 150 fathoms. Specific areas of occurrence of infected lobsters include Hudson, Block, Veatch, and Corsair Canyons—a range of over 300 nautical miles.

The nematodes (Figs. 1–5) are found coiled in lenticular cysts about 1 mm wide in and upon the anterior wall of the rectum. They occurred in 77 (25%) of 314 lobsters; intensity of infection ranged from 1 to 31 (mean, 3.5) per host; infection rates did not vary significantly with sex, size, or month.

The following measurements (means and range, in millimeters) are based on 21 specimens killed and fixed in hot (60 C) alcohol, cleared in glycerine, and mounted in glycerine jelly; 18 additional specimens, similarly killed and fixed, but cleared in lactic acid, provided superior resolution and measurements of the buccal capsule: Body length, 8.73 (7.24 to 10.41); maximum body width, 0.188 (0.129 to 0.246); body width at anus, 0.068 (0.058 to 0.079); length of buccal capsule, 0.060 (0.052 to 0.069); maximum width of buccal capsule, 0.019 (0.017 to 0.021); diameter of nerve ring, 0.041 (0.033 to 0.049); muscular esophagus length, 0.443 (0.346 to 0.575); muscular esophagus width, 0.023 (0.019 to 0.035); glandular esophagus length, 2.79 (2.24 to 4.00); glandular esophagus width, 0.109 (0.072 to 0.126); anus from posterior end of body, 0.127 (0.103 to 0.145); nerve ring from anterior end of body, 0.212 (0.168 to 0.248); excretory pore from anterior end of body, 0.269 (0.229 to 0.304).

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RESPONSE OF SALMONIDS TO LOW FREQUENCY SOUND

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The construction of dams in the Columbia River system for the production of hydroelectric power has created numerous problems for anadromous fish. Some of the difficulties relate to the loss of juveniles migrating downstream, which are unable to find their way through reservoirs or are injured as they pass through turbines or over spillways. In an effort to prevent this loss, the Bureau of Commercial Fisheries has been studying various methods of guiding these fish into collection facilities for passage around hazardous areas. This paper reviews past and current research on the use of sound as a method of guiding downstream migrating salmonids.

Burner and Moore (1953) exposed rainbow *(Salmo gairdneri)* and brown trout *(S. trutta)* to sounds between 67 Hz and 70,000 Hz at intensities up to 82 dB re 1 microbar. Moore and Newman (1956) conducted a similar study exposing juvenile salmonids to frequencies between 50 Hz and 20,000 Hz at intensity levels up to 7200 dynes/cm^2. These authors concluded there was no significant response to sound except for an initial "start" at the lower frequencies.

The California Department of Fish and Game* conducted a field study in which juvenile chinook salmon *(Oncorhynchus tshawytscha)* and striped bass *(Roccus saxatilis)* were guided into a bypass channel using a sound barrier constructed of 3- by 4-ft steel plates with air-driven vibrators attached. The number of fish entering the bypass increased from 52 per cent without sound to 90 per cent with sound for chinook salmon fingerlings and from 59 per cent to 80 per cent for juvenile striped bass. Subsequent attempts by Painter to guide fish in a river using a similar device were unsuccessful.

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* Personal communication from Richard Painter, California Department of Fish and Game, 1963.

In 1964 we attempted to guide steelhead trout *(Salmo gairdneri)* migrating downstream by using a sound barrier similar to that used by Painter. The study was made in an eastern Oregon irrigation canal that was divided into two channels, one 5 ft wide and the other 10 ft wide. The 5-ft channel served as a bypass when the barrier was in. The barrier (Fig. 1) was installed upstream from the 10-ft channel. It consisted of ten 3- by 4-ft steel plates mounted vertically and parallel to the flow of water. Air-driven vibrators were attached to alternate plates. These vibrators were driven at 270 Hz during the testing period. The frequency and amplitude of the sound generated by these vibrating plates were not measured. Painter measured the acoustic pressure 1 ft upstream from his installation and recorded an intensity of 97 dB re 0.0002 dynes/cm^2 falling off to 91 dB at 11 ft.

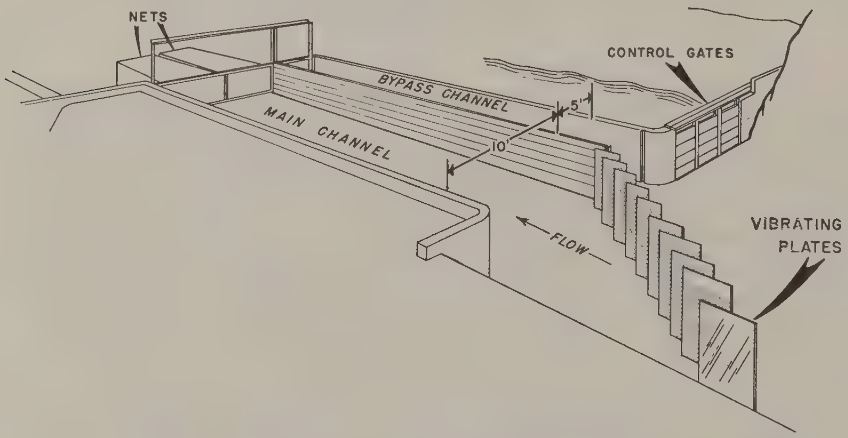

Fig. 1. Sound barrier system and evaluation facilities in irrigation canal near Umatilla, Oregon.

Before the sound barrier equipment was installed, 11 per cent of the steelhead migrating down the canal had entreed the 5-ft channel. After the installation, the number of steelhead entering the two channels was recorded for periods with and without vibration. An average of 77 per cent of the fish migrating through the canal during tests with vibration entered the 5-ft bypass channel, whereas only 33 per cent entered the bypass when the vibrators were off. The difference between the 11 per cent entering the 5-ft channel before the sound barrier equipment was installed and the 33 per cent after it was installed was probably due to the flow pattern created by the plates and to some extent by their guiding angle.

Following this field study, several laboratory experiments were conducted under a contract with the Boeing Company at Seattle, Washington. Juvenile chinook salmon were exposed to low frequency sounds of known frequency and intensity. The objectives of these experiments were to determine the frequency range in which the fish would respond, to measure the intensity necessary to elicit a response, and to describe the characteristics of the response.

These studies were conducted in two phases. In phase one, fish were placed in a sealed tank attached to an electromagnetic vibrator which was vibrated at various frequencies between 15 and 500 Hz. In phase two, fish were exposed to sounds between 5 and 500 Hz in an open channel with flowing water.

PHASE ONE STUDIES

Experimental Apparatus

The experimental apparatus for phase one consisted of an aluminium and plexiglass test chamber (Fig. 2) and an electromagnetic vibrator (force rating 7500 lb; maximum acceleration 100 *g*). The experimental chamber was mounted on a thick magnesium plate attached to the vibrator. The direction of vibration was horizontal and parallel to the long axis of the tank. Two pressure-sensing transducers were used to monitor the pressure

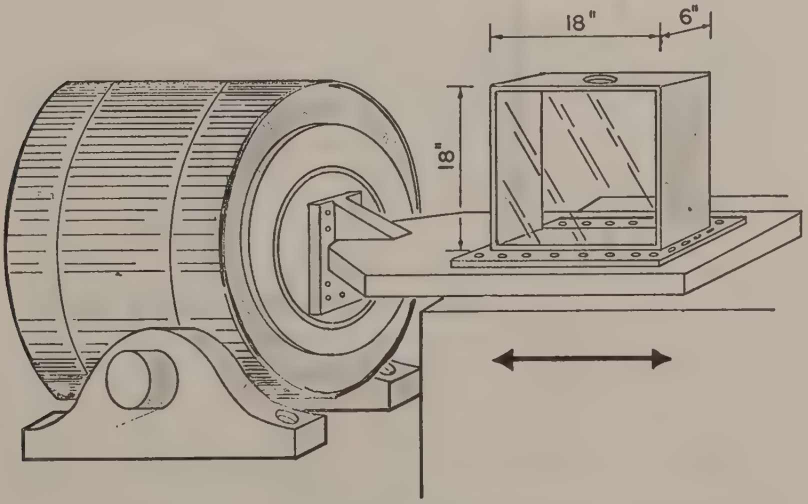

FIG. 2. Electromagnetic vibrator and test chamber. Arrow indicates line of vibration.

inside the chamber. An accelerometer was attached to the face plate of the vibrator to monitor the frequency and intensity of the vibration. The maximum acceleration used during these tests was 5 *g*.

Test Method

For each test the tank was filled with fresh water, after which five fish were introduced and the tank closed. No air was present in the tank during tests. Fish were held in the tank for 15 min before the vibrator was turned on. The response of fish to the specific frequencies and amplitudes were then noted. At the completion of each test, the exposed fish were removed; fresh water and non-exposed fish were then introduced for testing at another frequency. The dissolved oxygen content of the water in the test chamber was measured before and after each test. The minimum oxygen value recorded was 8 parts per million (ppm).

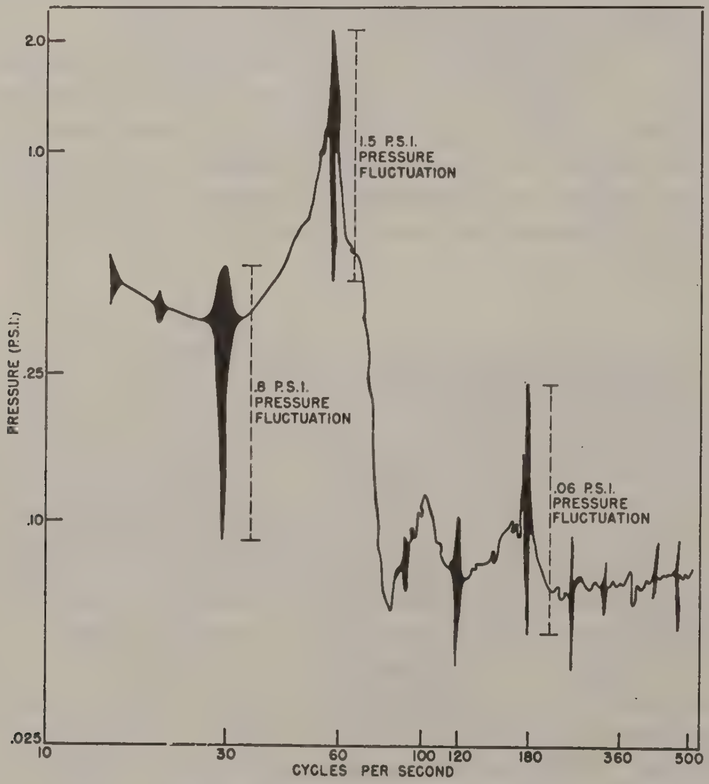

FIG. 3. Pressure within test chamber at frequencies from 15 to 500 Hz. Note fluctuation around 30, 60, and 180 Hz.

Observations

We noted two types of response. In one type, fish showed a loss of equilibrium, interrupted by short periods of erratic swimming. Characteristically, fish swam either on their sides, upside down, straight up or straight down, and often ran into the walls or into other fish. This loss of equilibrium occurred at an input of 30, 60, and 180 Hz with a 3 *g* acceleration; it was associated with a wide fluctuation in the pressure within the tank (Fig. 3). At an input frequency of 60 Hz, pressure fluctuated approximately 100 times per minute over a range of 1.5 $\mathrm{lb/in}^2$.

We described the second response as an escape action which was characterized by rapid swimming around the tank. Frequently the fish would place their snouts against the bottom corners of the tank and try to swim through the wall. The escape response was noted at several frequencies and at several acceleration levels; it was most pronounced at 70 and 88 Hz at an acceleration of 3 to 5 *g*. Fish exposed to these conditions would continue to swim until exhausted.

PHASE TWO STUDIES

Phase two studies were conducted in an open test channel with flowing water.

Experimental Apparatus

The wooden test tank (Fig. 4) consisted of two parts—a rectangular, endless raceway and attached anechoic chambers. The test portion of the raceway was separated from the anechoic chambers by a $\frac{1}{8}$-in. sheet of rubber (density 1.02). The sound source was located in the wall opposite the rubber sheet. Theoretically the sound wave traveling across the channel would pass through the rubber sheet into the anechoic chambers with a minimum of reflection.

A grid was painted on the floor of the test section to enable us to describe the response of the fish in reference to fixed points within the channel. Screens were installed to confine the fish to the test area of the raceway. A pump located outside the raceway created a water velocity of $\frac{1}{2}$ ft/sec through the test section. This velocity was fast enough to cause the fish to maintain an upstream orientation but not fast enough to tire them during the testing period.

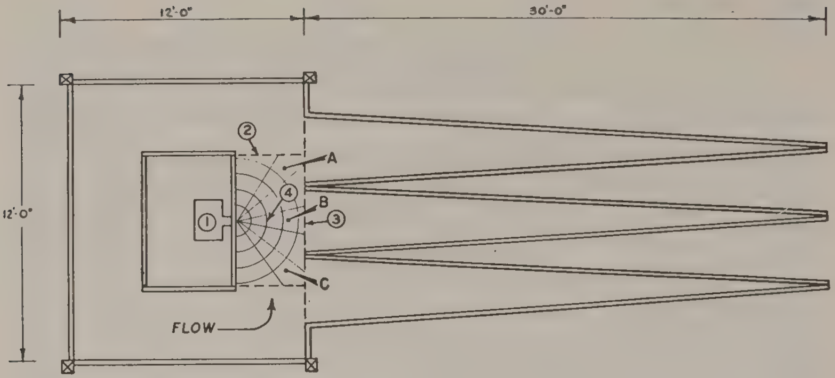
12'-0"
30'-0"
12'-0"
①
②
③
④
A
B
C
FLOW

FIG. 4. Plan view of endless raceway and attached anechoic chamber. A, B, and C are areas where fish response was recorded. Note position of following: 1, Vibrator; 2, Screen; 3, Rubber sheet; 4, Location of hydrophone.

Electronic Equipment

An electromagnetic vibrator with a force rating of 2250 lb and a maximum acceleration of 100 *g* was used to generate the pure tones used for this phase of the study (Fig. 5). The vibrator was attached through a hole in the wooden wall of the test section to a 6-in. disc mounted flush

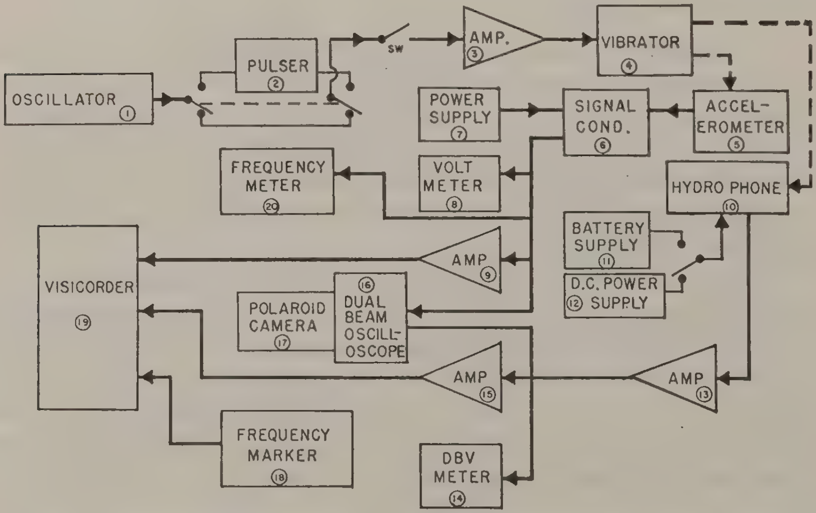
OSCILLATOR ①
PULSER ②
SW
AMP. ③
VIBRATOR ④
ACCEL-EROMETER ⑤
SIGNAL COND. ⑥
POWER SUPPLY ⑦
VOLT METER ⑧
AMP ⑨
HYDRO PHONE ⑩
BATTERY SUPPLY ⑪
D.C. POWER ⑫ SUPPLY
AMP ⑬
DBV METER ⑭
AMP ⑮
⑯ DUAL BEAM OSCILL-OSCOPE
POLAROID CAMERA ⑰
FREQUENCY MARKER ⑱
VISICORDER ⑲
FREQUENCY METER ⑳

FIG. 5. Block diagram of electric system used to generate and record sounds during open-channel tests at the Boeing Company, Seattle, Washington.

with the inside of the wall and joined to it by a rubber gasket. The system was capable of generating sine waves through the test frequency band with amplitudes well above the maximum of 160 dB re 0.0002 dynes/cm^2 used during this study. A hydrophone was mounted 2 ft from the wooden wall and 18 in. above the floor directly in front of the disc. The hydrophone was kept as this reference point during all tests with fish.

Test Methods

We exposed the fish to several patterns including sine sweeps, pulsed waves, and continuous waves before a final test design was chosen. At the conclusion of these exploratory studies, we designed an experiment to test fish for habituation resulting from repeated exposure to sound and to measure the response at particular frequencies.

Each group of fish was exposed to 22 test frequencies and three reference frequencies. The selected reference frequencies were 10, 70, and 240 Hz. These were used at the beginning, middle, and end of each test. A total of five tests using 47 different frequencies was completed.

To begin a test, 200 fish were placed in the test section for a 30- to 45-min acclimation period. Then the oscillator was set at the pre-selected frequency and the gain on the power amplifier increased until the acoustic pressure at the reference point reached 130 dB re 0.0002 dynes/cm^2. This procedure required about 1 minute. The power amplifier was then switched off. After 3 min, the power was turned on for 1 min, shut off for 1 min, and then turned on for two 10-sec periods separated by a 1-min off period. The next frequency was then set and the procedure was repeated for each of the 31 selected frequencies. Response of fish during the various exposures were noted by an observer. Each of the 1-min exposures was recorded on 16 mm movie film.

To prevent biased evaluation, the order of presenting the various frequencies was randomized and was not known to the observer until the test was completed.

Data Collected

The data we collected were limited to three sections of the grid as shown in Fig. 4. During the first exposure (1 min), we noted: (1) the direction the fish swam immediately after the sound was turned on, (2) the distance they moved away from the sound source, and (3) the amount of time they stayed out of the evacuated area. During the two 10-sec exposures, the observer recorded the furthest point of response from the sound source, All responses noted were avoidance responses.

Following a preliminary examination of the data collected in the above tests, several representative frequencies were selected, and pressure levels and wave shapes were measured at 165 selected points within the test section. Pressure at the reference point was maintained at 130 dB during these measurements.

Data Assessment

At the completion of the tests, it was necessary to assign a numerical value to each response so they could be compared at different frequencies. This was done in an effort to determine which frequency might be the most effective for repelling salmonids. To do this, each of four factors was weighed according to its relative importance to a general avoidance response.

The first factor was the swimming direction after the sound was turned on. Since practically all fish reacting to the sound swam laterally away from the sound source, this factor was not considered. The second factor was the time fish remained out of the evacuated area. Inasmuch as the time factor was extremely variable between different exposures at the same frequency, this measurement was also excluded. This left two factors—the farthest distance at which fish responded to the sound source and the area evacuated by the fish when moving away from the sound source. These two remaining factors were used to evaluate the degree of response to different frequencies. This was done by listing all combinations of values that could have occurred, beginning with the one arbitrarily determined to indicate the least valuable avoidance response. The least valuable response was when the fish gave a "start" reaction at 1 ft from the sound source but did not move away from it; the most valuable response was when all fish gave a "start" and vacated an area within 4 feet of the sound source. An intermediate response was one in which fish 4 ft away gave a "start" reaction and all fish within 2 ft of the sound source evacuated that area. We then assigned a numerical value to each response equal to its position on the list. This value is referred to as the computed value of fish response.

Fish Response

The second phase studies have just been completed and we are now starting a comprehensive evaluation of the data. For the present, several generalizations can be made.

Fish responded to the onset of sound from the lowest frequency tested up to 280 Hz; above this frequency no response was noted. The highest response values computed were obtained between 35 and 170 Hz. Figure 6 illustrates the response recorded for the section of the grid marked "A". Within this range of frequencies, the greatest distance moved away from the sound source was 2 ft. This occurred at 40, 70, 80, 100, and 120 Hz. The longest period the fish stayed out of the evacuated area was 60 sec.

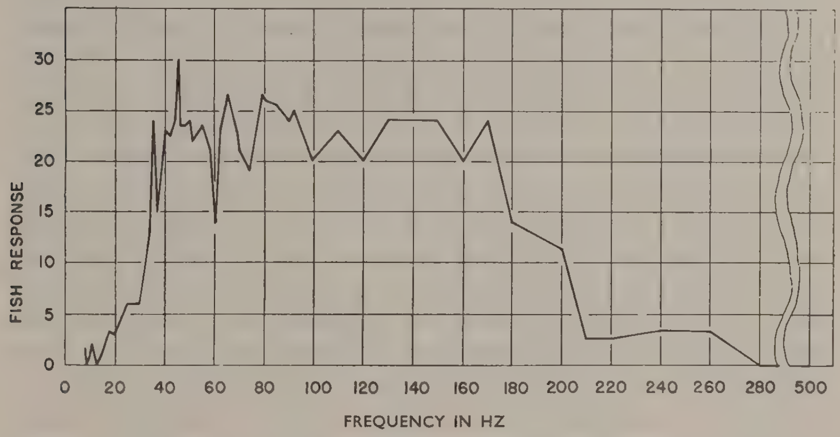

FIG. 6. Computed values of fish response to sound. Average of all data collected from section "A" of test tank.

This avoidance occurred at 80 Hz; the distance from the sound source was 2 ft. This period of evacuation was an exception; the fish usually resumed their normal distribution within 5 sec.

Our analysis of the response of fish to the reference frequencies shows that the fish did not become less sensitive due to repeated exposure.

A preliminary examination of the mapping data showed a wide variation in the intensity and form of the pressure field caused by a resonance of the wall through which the vibrating plunger was mounted and to a lesser degree by reflections. The lowest pressure was generally at the surface close to the rubber wall. An analysis of the wave shapes at different points indicated that a sine wave of the selected frequency was present in practically all areas of the tank.

Interpretation

Many attempts have been made to guide downstream migrating salmon using chemical, visual, and acoustical stimuli. None of these studies has resulted in the development of an efficient guiding system.

The results of the present studies indicates the possibility of repelling salmon with sound waves and the frequencies which may be best for this purpose.

In the field study conducted in the Eastern Oregon irrigation canal, fish responded to the sound in a way that caused them to move into the bypass. There are two theories that can explain this. The first theory assumes the fish can localize the sound and are repelled by it. If this is so, the fish would move as far away from the barrier as possible during their downstream migration and consequently move into the bypass channel. The second theory assumes the fish react negatively to the sound, but not being able to localize the source, swim to the bottom of the canal. If these assumptions are valid, the fish would have approached the barrier close to the bottom of the canal. Before we started the field study, we had recognized this possibility and had placed a 6-in. sill along the leading edge of the plate barrier. If the fish did approach the barrier close to the bottom they might have moved into the bypass channel by following this sill.

The results of the phase two study at the Boeing Company lend support to the first theory. The initial response of the fish to frequencies between 35 and 170 Hz was to swim away from the sound source; however, they would soon wander back into the vacated area. The possibility of the fish recognizing the primary source of sound within the test chamber after the first 2 or 3 sec is remote due to the many reflective surfaces within the tank.

Severe physical problems are encountered when experimenting with low frequency sound in a small tank. This makes it difficult to obtain useful information about a fish's ability to localize a sound source using the behavior study technique. Future workers should consider working in a free field environment or plan on making a major effort in the development of an anechoic test tank.

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DISCUSSION

Dr. van Bergeijk: The first comment that should be made on this paper is, I think, that it is an example of what I would call "biological engineering". The effort is directed primarily at solving a specific problem: how to keep fish out of generators. As such, it is partly based on common sense and good-old empiricism, and wholly unsuccessful, so far. Which should not discourage one; problems are often more interesting by virtue of being difficult.

As to specifics, it seems to me that the pressures you measure in the phase 1 experiment are actually irrelevant. If you accelerate a mass of water contained in a non-rigid container, you can't help developing pressures, of course; but from what we know about equilibrium functions it would appear that the acceleration itself is the relevant stimulus, while any pressures developing incidental to this have negligible effect. In other words, the phase 1 experiment does not demonstrate sensitivity to sound pressures, I think, but simply shows that, given sufficient acceleration, fish will become disoriented, or will exhibit signs of discomfort. Whether what you see can really be interpreted as an "escape reaction" seems a bit questionable to me without further substantiation. If it is indeed an escape reaction, the question is raised whether it could be used commercially. Here I have a crucial question: how much power is required for evoking the reaction? With the volume of water to be moved at these accelerations, you may be consuming a significant part of a generator's output!

The phase 2 experiments seem quite straightforward; the sound source generates a considerable near-field displacement, and the measured pressure, though probably proportional to the stimulus events, is a complex quantity due to the near-field pressure, the free-surface motions of the water and any residual reflections in the tank. I would suggest that the effective stimulus in this case is not the pressure but the near-field displacement (or a derivative function of it), and that the receptor organ is the lateral line. The 2 ft maximum escape-distance strongly suggests a near-field ($1/r^2 - 1/r^3$) attenuation.

Two feet is not much distance in a fast-flowing river, but if a barrier could be constructed of these vibrators, the problem would be solved; it would be much less formidable in its power requirements than the shaking plates. But I have another suggestion,

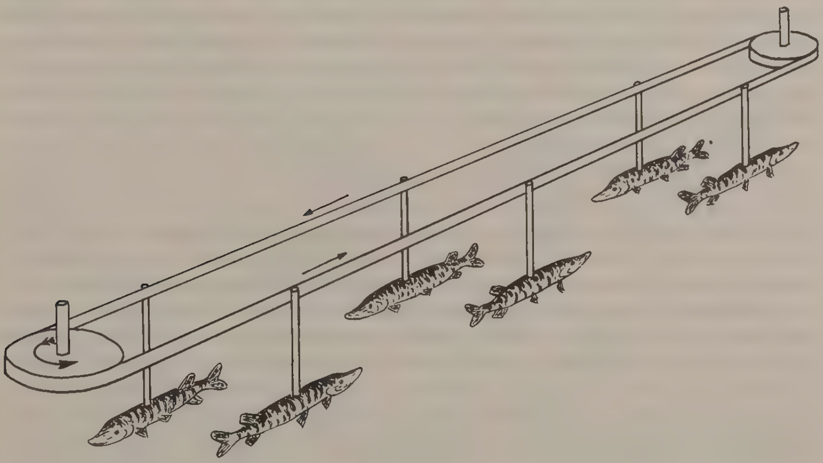

Fig. 6.

once it seems to be the case that the lateral line can be used as a channel for the communication of discouragement. Why not put some pike or muskie in wire live boxes across the channel? That way you optimally utilize the little fish's powers of recognition; the few lunkheads that don't flee will keep the pike alive. Since the logistics of keeping this sort of system working for extended periods are a bit hairy, I have thought of another system that is shown on Fig. 6. As you can see, a number of plastic pikes are parading like sentries across the channel, driven by a continuous conveyor belt. If driven at realistic speeds, these objects will generate near-field displacements every bit as large as the vibrators you are thinking of, and they have the additional advantage of stimulating the lateral line of the fish in just the right way to evoke inborn or learned predator-escape responses. How big this last factor is remains to be measured, of course. The power requirements and overall cost of this set-up would be quite minimal; in fact, it could be driven directly by a water wheel operated by the current in the channel.

MR. VANDERWALKER: As far as a near field effect is concerned, I want to emphasize that all the reactions of the fish that I observed occurred within the near field.

Fish do not usually swim downstream, they face upstream and let the current carry them, and it's very simple for them to avoid an object by increasing their swimming speed and simply turning away at an angle.

On the pressure measurements, I know that our measurements were inadequate in that we were only able to measure pressure. I would be very encouraged if anyone here would be able to tell me how I can measure the directional movement of the water in the near field because this is what I'd like to be working with.

DR. SHAW: The fundamental contribution of this paper by Mr. VanDerwalker is that he is one of the first, among the fishery biologists, to obtain from fish an avoidance response to low frequency sound. However, from the paper it is not clear if the response is to pressure waves, low frequency sounds, or related phenomenon, such as water displacements or resonance from the tank walls.

A review of the problem of fish guiding shows that it has been a serious problem among fishery biologists since the construction of hydro-electric dams on the Northwest coast of the United States. There have been a number of approaches to the problem and the need is of obvious importance, since 20 to 60 per cent of migrating juvenile fish, those migrating from the lakes and rivers into the sea, are destroyed when they must pass the entrapments inadvertently produced by the power plants. The problem has been approached several ways, either by utilizing the sensory capacities of the animals, to redirect ("guide") them, or by creating a physical barrier to deflect them. Brett, in a comprehensive review a number of years ago, pointed out that guiding is often applied to several techniques, namely attracting the fish to a particular object, inducing fish to orient in a D.C. electrical field, or frightening fish away from a damaging turbine or spillway. Actually, what is frequently involved in the attracting phenomena is approach of the fish to a stimulus of low intensity. In fright situations the animal is withdrawing from a stimulus of high intensity. Often, in the latter case the behavior of the animal, once it withdraws, is generally random and "helter-skelter". This *sometimes* can be utilized in diverting the fish from deadly objects. In the experiments presented by Mr. VanDerwalker therefore, guiding is an "escape reaction"—actually, it is a withdrawal from an apparently high intensity stimulus. In previous work two other authors working with sound frequencies, ranging from 60 Hz to 70 kHz, showed that these frequencies produced only a "start" effect, particularly in sounds of lower frequency, whereas there was no observable response to sounds above 15,000 Hz. The experiments were carried out in an open field in contrast to the more restricted test conditions of Mr. VanDerwalker's experiments. Those authors were unable to find a way in which the fish could be redirected into a bypass. Through the utilization of other sensory inputs, other methods have been tested to guide fish. These methods had to be economically feasible and technically possible. Some of the methods and their results are given below. A light source, such as a light beam or light of various intensities, gave little if any deflection of fish into a bypass (by deflection, I mean Brett's deflection of 75 per cent which is considered to be a good result). Fish entered the light field, remained there temporarily and then continued on their way. Amber or blue light has no noticeable effect but a curtain of air-bubbles with reflecting light proved to be a successful deflector—unfortunately, technically difficult. Sound was effective when light was on but did not seem to affect behaviour when the fish were in darkness. The time of darkness is when most of the migration takes place.

Odor was also tested, skin rinses of humans, and formalin, but again there was no appreciable effect. Bursts of methylene blue dye during daylight was fairly effective in deflecting the fish but only at the instant of burst. Here again is another example of a stimulus that causes, because of its high intensity, a withdrawal of the animal, but the fish quickly became adjusted and evidently no longer responded with avoidance behavior. One of the more effective techniques has been that of hanging chains at intervals of two or more inches. The physical presence was not as critical as their light reflecting properties, and fish tended to avoid the light reflections. Many of the stimuli presented to the fish have the common property of high intensity levels thereby causing a withdrawal of the fish. Actually the ideal situation would be the use of a stimulus of low intensity which would attract the fish and once the fish have approached the stimulus, they would remain oriented to the stimulus until they were well out of the area of danger. An effective method that employs this principle is a moving curtain of cables. The fish tend to take a fix on the moving curtain and are effectively guided—without any alarm reaction. My own researches have indicated that this is a workable idea, since in a classic optomotor response, fish orient to a moving field of black and white vertical stripes. The fish move at the same speed as the moving stripes and move constantly in the same direction as the stripes.

Thus, in fish guiding a number of ways have been tried. The final question remains, whether or not, in the problems of fish guiding, sound is indeed the best technique. It may be the best technique in terms of technical efficiency and cost, but in terms of truly guiding the animal without causing an intense reaction on the part of the animal, it may not be as effective as a visual stimulus.

MR. VANDERWALKER: We've tried lots of methods, including air bubbles, electricity, and we're not as optimistic as Dr. Brett. In order to maintain the present population levels, we're going to have to save 90—95 per cent of the fish.

The reason we're trying to use sound is because the other methods are extremely costly to build and maintain. Physical barriers, such as screens, which are commonly used now, cost a tremendous amount of money, and we thought that if sound were successful, we might be able to build something that was less expensive.

DR. MACKAY: In the second part of your experiments, did you simply switch in a sound source, or did you raise it gradually? Was this a startle reaction or an avoidance reaction?

It seems to me that there's a very interesting aspect to the experiments of this type, namely which way would a fish take off?

In an analogous situation, it's not interesting that the human eye focuses, but how it knows in which direction to get into focus that's of interest. Similarly with the ear. If a fish is suddenly immersed in a sound source, how does it know which way to go to go to a region of lower intensity? I think this is truly of interest. Is there a gradient of something along the fish that it is able to sense?

MR. VANDERWALKER: During our study we switched the amplifier in directly; however, during our preliminary studies we tried turning up the volume manually and found little difference between this reaction and the reaction to the sound when the amplifier was switched on to full power.

MR. FITZGERALD: It seemed to me you were talking about a barrier, not guiding the fish. Did I hear you right you said you had a source level of 160 dB?

MR. VANDERWALKER: Our maximum recorded pressure was 155 dB re 0.0002 dynes/cm^2.

MR. FITZGERALD: Did you observe any cavitation?

MR. VANDERWALKER: Not during the experiments we conducted, but in preliminary tests of the tank when we were practically shaking the entire area we did.

MR. FITZGERALD: At the source?

MR. VANDERWALKER: At the source.

MR. FITZGERALD: Have you ever tried setting up a cavitation barrier?

These forces on the fish would be quite terrific and they might be quite effective, and you can focus this.

MR. VANDERWALKER: No. Our experience in cavitation has been confined to its occurrence in turbines. There is evidence that this type of cavitation is harmful to fish.

DR. VAN BERGEIJK: Why didn't you use air screen? It's very simple to develop. A screen of air bubbles.

MR. VANDERWALKER: I've done quite a bit of testing with the air screen. I was able to guide 95 per cent of the fish during the day time, but at night the fish could not be guided. This indicates the response was a visual one and not a response to the sound waves associated with the air bubble screen.

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A CRITIQUE AND MANUAL FOR A NEW TECHNIQUE IN INDUCTIVE SALINOMETRY

by

John W. Van Landingham

ABSTRACT

The potential reliability versus existent reliability of portable inductive salinometers is discussed. Variable cell geometry is stated to be one of the chief sources of error. This variability can be significantly decreased by employing a new operational technique, which is described in the manual of technique.

INTRODUCTION

Oceanographic salinometry is experiencing an irreversible evolution in methodology. The transformation, a result of an increasing need for more salinity data, less tedium for the analyst, and greater freedom from subjectivity, is continuing at an accelerating pace. This trend, which has grown from infancy to maturity within the past decade, began in earnest with the publication of a paper by Hamon and Brown (1958) describing an in situ salinometer.

Subsequently, laboratory instruments (generally console types) were developed. More recently the use of less expensive portable models has gained impetus, and the following discussion is concerned solely with this latter type of instrument.

Early salinometers were beset with many problems, most of which were mechanical. The greater proportion of faults has been reduced by better engineering and design, but reports that data fall short of the quality expected from the instruments continue to appear.

Cox and Folkard (1964) analyzed discrepancies between replicate analyses performed on different salinometers. Although their work has shown that a large proportion of this disparity reflected an error in conversion tables, corrected data from the two sources still show significant scatter (the standard deviation for 50 determinations was 0.004%). This variation, however, was less than the error limits permissible with our present definition of salinity (Sverdrup, Johnson, and Fleming, 1942).

In 1963-64, participants of the International Cooperative Investigations of the Tropical Atlantic (Austin, 1963) undertook an intercalibration program to assist in the evaluation of salinity data collected during the EQUALANT surveys in the tropical Atlantic. Unlike Cox's work, this study was a comparison of replicate salinity determination among laboratories rather than among instruments. The procedure involved the routine analysis at each participating laboratory of two intercalibration standards of dissimilar salinities. The following statistics were obtained for each of the standards:

Standard A (low salinity)	Standard B (high salinity)
n = 14	n = 14
S = 0.0107%	S = 0.0217%

where

n = number of data points (13 salinometer determinations plus ICES (International Council for the Exploration of the Sea) titration)

S = standard deviation (root mean square deviation) of the samples.

DISCUSSION

Certainly volumes of erroneous salinity data, recognized or not, must clutter the files of most marine laboratories. Is this lack of quality an inherent weakness in the inductimetric method or is it rather a result of the technique applied to the analysis? The results of several years of

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*Contribution No. 44, Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida 33149.

experience in the field with this type of instrument suggest that once an instrument has been freed of defects from an engineering standpoint, it is capable of providing nearly perfect precision, even under rigorous field conditions.

If the electronic components of the salinometer are functioning properly (and reliability has been demonstrably high in recent years), then precision depends primarily on stable cell geometry. (Cell geometry is herein defined as the internal volume, configuration, and homogeneity of the fluid matrix—sea water.) Accuracy is predominantly a function of stable geometry and internal thermal drift.

The greatest single cause of geometric instability of the cell is the presence of occluded gases in the medium. It is impossible to remove these gases quantitatively from the sample. The technique may be controlled, however, so that the volume of bubbles is small and the sensor is not affected by their presence. Constant cell geometry depends upon two important factors:

a. Immaculate cleanliness of the cell.

b. Uncompromising care in use of degassing technique.

The first of these requirements is easily met. Our experience has shown that the cell must be chemically cleaned at intervals of every 20 samples. Apparently, invisible films of oils in the sea water adhere to the cell components and create poorly wetting surfaces. This condition leads to more cross-contamination between samples and increases the entrainment of occluded gases. We clean the cells by filling with alcoholic solutions of common detergents and stirring for 5 minutes. Many other combinations probably would be equally effective. Meeting the second requirement, effective degassing depends in part upon fulfilling the first requirement, but more upon the technique by which the cell is filled.

The author has developed a technique which, when rigorously followed, yields nearly perfect replication of conductance values. The first step of this procedure is to eliminate use of the pulsating vacuum pump furnished with the instrument and to replace it with a continuously regulated supply from a venturi source (figure 1).

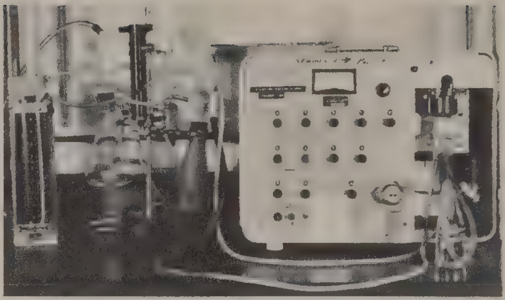

Figure 1. Detail of Apparatus, Including Vacuum-Regulation System

This arrangement is accomplished by connecting the exhaust line from the mechanical pump to the input of a laboratory model filter pump. This system provides a gentle, steady vacuum while the instrument is in the analytical mode. At the beginning of the sampling mode, vacuum within the cell lifts the sample and removes occluded and dissolved gases from the system. Additional benefits of this technique are elimination of one operation in the sequence (switching on the pump motor) and reduction in flux of motor heat through the system.

Gas bubbles, either microscopic or macroscopic, tend to form in areas of turbulence. The cell has three such critical areas:

a. The constriction of the bore of the sampling stopcock.

b. The constriction of the throat at the base of the toroid.

c. The constriction of the shaft well at the top of the cell, which houses the stirring shaft and the overflow exit.

The worst of these areas is the stopcock bore; the purging process must take place above this area. Should the sample be accidentally lowered below this point, the process should be started again.

Experience has shown that a reading made on the first fill without prior purging is almost always in error, even though a steady galvanometer pointer would indicate stability. Effective degassing is accomplished by raising and lowering the sample interface repeatedly past the second turbulent area, the base of the toroids.

This "ebb-and-flow" technique should be carried out after the preliminary filling and adjustment of the instrument (described in detail later, in the manual of technique).

After two or three such passes to expel occlusions, the cell is filled with the sample. As the sample enters the upper stricture of the shaft well, a large bubble of air is certain to become trapped in the lumen between the shaft and the wall of the cell. If this bubble is not removed, the starting torque of the stirrer will break it into tiny bubbles that will be unevenly dispersed throughout the sample by impeller action. Fortunately this bubble can be expelled if pressure upon the sample is maintained while the stirring motor is started. The spin of the shaft is communicated to the sample, and the combination of pressure and centrifugal force squeezes the bubble out through the overflow line.

The analytical procedure was developed to its present state during a cruise of the FWS R/V Geronimo. From January 30 to February 7, 1966, the vessel occupied 13 hydrographic stations. Each station included an 18-bottle Nansen cast to a depth of 500 meters. The salinities were analyzed on board after the samples came to equilibrium with the temperature of the laboratory.

The data progressively improved as the technique was developed. Replicates of the conductivity ratios on the last 2 of the 13 stations agreed within ±3 × 10^{-5}. Only one value of each set of these replicates was recorded. The data from these two stations were part of a scheduled time study and were excluded from the statistics discussed below. Included in the statistics were the results of 282 determinations by the new technique (group B). Also included were 60 determinations (from the first two stations) made by the conventional technique, and 32 observations (scattered throughout the series) made by a technique intermediate between the conventional and the new (group B).

The statistics are summarized as follows:

	All samples	Samples analyzed by conventional technique (Group A)	Samples analyzed by new technique (Group B)
n	374	92	282
S	0.0019%	0.033%	0.0010%
$\bar{d}$	0.0011%	0.026%	0.0006%

(n = sample size; S = standard deviation of the sample; $\bar{d}$ = average of the deviations of duplicate samples from their mean.)

The effect of technique on the precision of the data is apparent.

We should now examine the statistical treatment more critically, to verify, if possible, the significance of the increased precision. The statistical population of interest is the differences (y) between replicate samples rather than the actual salinities. The sets of values in table I suggest the hypothesis that we are dealing with two discrete samples of different populations, each with its characteristic parameters.

The "F-test of hypothesis" involving the

TABLE I. COMPARATIVE STATISTICS FOR CONVENTIONAL (GROUP A) AND HIGH PRECISION (GROUP B) SALINOMETRY TECHNIQUES

Group	n	$\bar{y}$ (%)	$\frac{\sum(y_i - \bar{y})}{n}$ (%)	$\sum(\bar{y}_i - \bar{y})^2$ (%)	$s^2 \times 10^3$ (%)	$s \times 10^3$ (%)
A	46	0.0053	0.0289	0.6972	0.0155	3.94
B	141	0.0013	0.00108	0.2866	0.00205	1.43

TABLE II. TYPICAL CONDUCTIMETRIC AND SALINITY DATA OBTAINED DURING GERONIMO CRUISE 7

Sample	Conductivity Ratio	Corrected Salinity
Substandard	1.02554	---
1	1.02197	35.867
	1.02195	0.866
2	1.02182	35.861
	1.02183	0.861
3	1.02750	36.085
	1.02751	0.085
4	1.04102	36.621
	1.04108	0.623
5	1.03980	36.572
	1.03979	0.572
6	1.05067	37.003
	1.05068	0.003
7	1.04859	36.921
	1.04862	0.922
8	1.04656	36.839
	1.04660	0.841
9	1.04521	36.786
	1.04522	0.787
10	1.04398	36.738
	1.04398	0.738
11	1.04259	36.683
	1.04263	0.684
12	1.03203	36.264
	1.03205	0.265
13	1.02769	36.093
	1.02773	0.094
14	1.00904	35.357
	1.00905	0.357
15	1.00143	35.056
	1.00143	0.056
16	0.99494	34.802
	0.99486	0.798
17	0.99143	34.663
	0.99145	0.664
18	0.99352	34.745
	0.99355	0.746
Substandard	1.02555	---

sample-variance ratio (Li, 1957) indicated that the variances of the two subgroups were significantly different at the 1% level.

Since both the variances and sample sizes were unequal, the approximate t-test (Li, 1957) was used to examine the significance of the differences between the means. The value $t^1 = 6.745$ was significant at the 5% level.

These tests indicate that the new technique gives a significant increase in the precision of the conductivity-ratio measurements. This higher precision is now obtained routinely at this laboratory.

The high degree of repeatability of the conductivity ratios is apparent in table II, showing data from the cruise.

It must be remembered that precision in itself offers no guarantee of accuracy. Occasionally systematic errors creep into the analysis, and the chemist must always be on the alert for them. Table III is a reminder of this fact. The data consist of comparisons between titrimetric and salinometric analyses on the same randomly selected samples. Of the 19 stations represented, data from 4 (asterisk) contained systematic errors that would not have been suspected without the quality-control analyses.

MANUAL OF TECHNIQUE

1. Connect pump exhaust to vapor inlet of a venturi water pump.

TABLE III. SALINOMETRY DATA SHOWING THE DETECTION OF SYSTEMATIC ERROR IN HIGH PRECISION SALINOMETRY BY QUALITY CONTROL TITRIMETRY

Sample No.	Salinometer Value (%)	Titrimetric Value (%)	|ΔS| (%)
1057	35.797	35.803	0.006
1061	36.470	36.449	0.021
109	35.667	35.678	0.011
120	34.900	34.890	0.010
112	35.698	35.706	0.008
860	35.466	35.404	0.062*
868	35.653	35.598	0.055*
663	34.846	34.848	0.002
675	35.006	34.988	0.020
678	34.442	34.432	0.010
366	35.881	35.873	0.008
371	34.339	34.317	0.022
663	34.846	34.848	0.002
675	35.006	34.986	0.020
678	34.442	34.432	0.010
509	35.879	35.801	0.078*
518	35.058	34.994	0.064*
49	34.978	34.985	0.007
68	34.644	34.623	0.021
*Systematic error.			

2. Fill cell with detergent solution and stir for 5 minutes. Empty and rinse with fresh or distilled water.

3. Wipe off glass sampling tube, turn stopcock to "Fill" position, close air bleeder vent with finger, then insert sampling tube into supply of previously used Copenhagen water.

4. When the water rises to a level about 1/4 inch from the bottom of the cell, turn stopcock to "Discharge" position and empty the cell. Fill the cell completely with used Copenhagen water, then discard.

5. Insert sampling tube into fresh Copenhagen water. (Always wipe exterior of sampling tube dry before insertion into any sample for the first time.) Repeat step 4 (the rinsing procedure only).

6. After rinsing the sampling tube with fresh Copenhagen water, adjust the conductivity-ratio dials to read the known conductivity ratio of the Copenhagen standard. Raise the bottle (or ampoule) of the standard and permit the level to rise (by gravity) until the bottom half of the toroid is immersed (figure 2). Without changing the stopcock position, place finger over the air bleeder opening; lower the bottle well below the level of the instrument. Intermittently bleed just enough air into the system to permit the liquid level to drop to a point just below the bottom of the toroid.

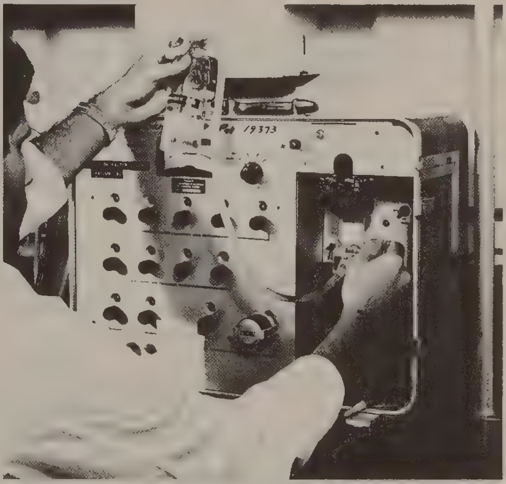

Figure 2. Proper Technique for Introducing Sample into the Cell

7. Raise the bottom, remove finger from bleeder, and continue to fill cell by gravity. As the rising sample enters the shaft well at the top of the cell, start the stirrer, maintaining positive hydrostatic head on the cell by keeping the sample bottle elevated. Turn stopcock to "Hold" position, then lower the bottle to the

bench, leaving the sampling tube in the sample. Obtain and record the temperature of the cell contents, adjust the temperature compensation dial, and make a *preliminary* adjustment of the standardization dial. *Stop stirrer*.

8. Using the technique described in step 6, lower the level of liquid and continue to purge the gases by two or three successive passes over the bottom of the toroid. Refill exactly as before. With the function switch in salinity mode, readjust the standardization dial.

9. Stop stirrer. Lower sample to just below the bottom of the toroid, refill as before, and check the null point galvanometer. Allow a few *seconds* for equilibrium to be established. Only a very minor adjustment should be necessary at this point. Frequently none is required. THE ANALYST SHOULD NOT PROCEED FURTHER UNTIL THE STANDARD READING IS PERFECTLY REPRODUCIBLE.

10. Stop stirrer and drain contents of cell through filling tube into used Copenhagen water supply.

11. Replacing the Copenhagen standard with substandard water (drift control standard), repeat steps 3 through 6.

12. Fill the cell as prescribed with substandard water, place function switch in salinity mode, and make preliminary adjustments on the conductivity-ratio dials.

13. Stop stirrer and repeat steps 8 and 9. Following completion of step 9, turn function switch to temperature and observe and record the temperature.

14. Stop stirrer, lower sample, and refill and check conductivity ratio. If change is not significant, drain substandard water from the system and proceed with the analyses, using the same procedures. Accept only reproducible (<±10 × 10^{-5} conductivity-ratio units). Data showing greater divergence reflect geometric instability of significant proportions.

15. At the end of a series of not more than 20 samples, run a replicate of the same sample of the drift control substandard.

16. Before another series is started, the cell should be scrubbed with detergent.

Time required per determination is about 1.8 minutes for the new technique as compared with 0.8 to 1.2 minutes for the old. Since the standardization procedure is subject to the same problems and errors, the prescribed modification is mandatory for standardization to reduce systematic error, which would result from faulty adjustment of the instrument.

In conclusion, the writer believes that the salinometry instrumentation now available is capable of producing a significant increase in the quality and reliability of salinity measurements. Much of the difficulty experienced in obtaining high-quality data may be attributed to faulty operating techniques, which produce unstable cell geometry.

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N. Y. STATE CONSERVATION DEPT.
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THE N. Y. STATE CONSERVATIONIST

Fishery Picture Changing In Lake Erie

Pollution A Major Factor, Survey Shows

by Harry D. Van Meter and William F. Shepherd*

ACTIVITIES of the research vessel *Musky II* during the past two summers created a series of rumors along the shoreline of Lake Erie from Barcelona to Buffalo. Word had spread that the salvage operations of local treasure hunters were under surveillance.

Others, more in the know, speculated that the vessel and its crew were either keeping tab on the catch of commercial fishermen or checking the source and extent of pollution. None of these reports were correct. In reality, fishery-limnological surveys were being conducted by research biologists of the U.S. Bureau of Commercial Fisheries. Although headquartered in Sandusky, Ohio, their vessel operations cover the entire lake. The staff works closely with the biologists of the several state agencies and the information that is obtained benefits all fishermen, whether they be sport or commercial.

A typical 2-week cruise in New York waters in September, 1965 was followed by a similar visit in June, 1966. The objectives of these cruises were: To determine changes in the fish population and environmental conditions in recent years; to determine if the geographic and depth distributions of certain species of fish in the summer differed from that in the autumn; and, to obtain much-needed information on the selectivity of experimental gill nets, particularly for the fresh-water drum (sheepshead) and the walleye.

These exploratory ventures yielded considerable information that was surprising and interesting. Several thousand fish of 23 different species and of various sizes and ages were caught with bottom trawls, fyke nets, and experimental gill nets. The gill nets were fished in 1,100-foot gangs. Each gang contained equal lengths of netting ranging from 1- to 6-inch mesh (stretch measure) in half-inch intervals. Bottom trawls were 25-foot semi-balloon nets with small-mesh cod ends that were dragged for 10-minute periods. The fyke nets had standard 4-foot diameter hoops and 50-foot leads.

A typical catch from a 10-minute tow of a trawl net from the research vessel Musky II

> *Lake Erie fishery research is currently being co-ordinated through a group known as the Lake Erie Fishery Commission. Members of the committee are the Ontario Department of Lands and Forests, the Michigan Department of Conservation, the Ohio Division of Wildlife, the Pennsylvania Fish Commission, and the New York Conservation Department. The U.S. Bureau of Commercial Fisheries, an ex officio member, advises and assists. Administrators and fishery scientists of these agencies meet each year to co-ordinate their research and to review progress of studies that are being conducted.—Editor*

Contribution No. 356, Ann Arbor Biological Laboratory U. S. Bureau of Commercial Fisheries.

Biological information such as length, weight, and sex were recorded for many of the fish captured. Scale samples were taken from individuals of all major species for determination of the age of the fish and rates of growth. In addition, the digestive tracts of certain specimens were preserved for food and parasite analyses in the laboratory.

Fish Seem Constant

In general, the kinds of fishes, and the geographic and depth distribution of the catches in the eastern basin in June, 1966 did not differ greatly from those in September of the preceding year. The numbers of some fishes, however, had changed — the so-called trash fish were more abundant and the more desirable commercial species were less numerous than in 1965. Yellow perch was by far the most abundant species in the catches. Other fishes taken frequently included white suckers, stonecats, white bass, smelt, and walleyes. Sizeable populations of smallmouth bass and fresh-water drum were also found.

As a rule, most fish were caught where the water was 20 or more feet deep. This concentration was caused by the abundance of yellow perch in the area and the fact that they were congregated largely offshore. Walleyes and smallmouth bass, on the other hand, were taken much more frequently on the rocky ledges and reefs in the shallower, shoreline waters. Most of the walleyes on these shoals were the younger fish — the larger and older ones were usually captured beyond the 20-foot depth.

Analyses of the lake water also played an important part in the surveys. Comparatively speaking, the waters in the eastern basin are much clearer than those of the western basin. Transparency readings usually measured from 8 to 20 feet, depending on the location and the roughness of the seas. Similar readings in the southwestern corner of the lake in the same season might range from 6 inches to 3 feet. During the survey in the fall of 1965, the water was stratified thermally at about 40 feet but the deeper layers had sufficient dissolved oxygen to support aquatic life. Furthermore, the deeper waters showed neither thermal stratification nor low oxygen levels at any location in the summer of 1966.

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*Mr. Van Meter is a Fishery Research Biologist with the U.S. Bureau of Commercial Fisheries at Sandusky, Ohio; Mr. Shepherd is Regional Fisheries Manager for the New York State Conservation Department at Olean, New York. The photos were taken by Harold A. Robins of Westfield, New York.

"There is considerable evidence, however, of increased enrichment of the eastern basin compared with conditions that were found in similar surveys made more than 5 years ago by the research vessel Cisco of the Bureau of Commercial Fisheries. During the past two years large mats of filamentous algae have been seen extending out from shore for some distance and many beaches are fouled with decaying masses of this vegetation. This condition, in itself, is an indicator of the dissolved (and invisible) nutrients in the water that owe their origin to the large volume of human wastes discharged into the lake by the Detroit River and along the lake shore."

Increased Pollution Revealed

There is considerable evidence, however, of increased enrichment of the eastern basin compared with conditions that were found in similar surveys made more than 5 years ago by the research vessel *Cisco* of the Bureau of Commercial Fisheries. During the past two years large mats of filamentous algae have been seen extending out from shore for some distance and many beaches are fouled with decaying masses of this vegetation. This condition, in itself, is an indicator of the dissolved (and invisible) nutrients in the water that owe their origin to the large volume of human wastes discharged into the lake by the Detroit River and along the lake shore.

In spite of increased evidences of pollution, the biologists were encouraged by the results of the two surveys, particularly in the continuing productivity of desirable fishes in these waters. Walleyes, which were plentiful, are believed to be a sub-population distinct from walleyes that live in the western basin of the lake. They differ from the western basin fish in growth and condition and their numbers, from year to year, appear relatively stable. All-year classes are well represented in the commercial landings — a condition that suggests a greater frequency of good hatches than in the sub-populations of walleyes in the western end of the lake. This stability in the walleye population is reflected in a commercial production from the New York waters that has remained between 60,000 and 107,000 pounds per year for almost a decade.

The U.S. Bureau of Commercial Fisheries vessel Musky II

"Picking" the nets is a part of a day's activity

The commercial landings of all species in 1966 totaled 220,000 pounds. Of this catch, 105,000 pounds were walleyes, another 105,000 pounds were yellow perch, and the remaining 10,000 pounds consisted primarily of white bass, suckers, burbot, carp, and sheepshead. This figure is well below the average annual production of 852,000 pounds of commercial fish landed in New York waters of Lake Erie in the period 1935-1966. Until 1956 commercial landings at New York ports frequently ranged from 1 to 2¼ million pounds per year and never fell below about a third of a million pounds.

Decline Of Fishery

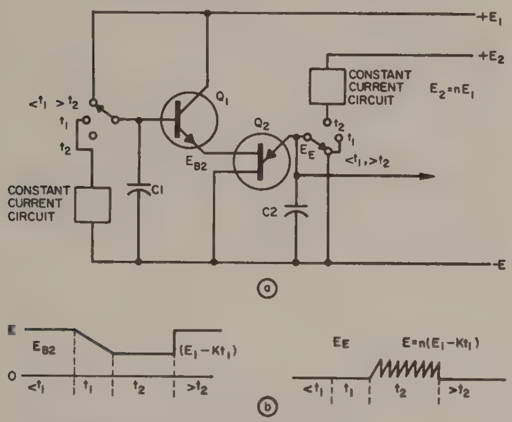
Beginning in 1957, however, the production of fish from the New York waters of the lake declined steadily to about a quarter-million pounds in 1963 and has remained at that level since. This decline in the fishery is probably due, in part, to the disappearance of certain "high-value" fishes such as the blue pike and the whitefish, and, in part, to the rising costs of fishing operations. Fishing effort has declined, in fact, until today only a handful of New York commercial fishermen are left on the lake.

Commercial Fishing Can Revive

This depressed condition of the commercial industry need not exist. The walleye population has apparently grown to fill the space formerly occupied by the blue pike, and yellow perch and other marketable fishes are abundant. Whether these fish populations can support a profitable and healthy commercial industry in spite of the high cost of labor and fishing equipment remains to be seen. Substantial numbers of desirable fishes are present in the eastern basin, however, and the outlook is good for both the sportsman and the few commercial fishing enterprises still in business.

A/D multiplier/divider has UJT as relaxation oscillator

A simple multiplier/divider is based on the unijunction transistor as a relaxation oscillator. A simplified block diagram (Fig. 1) illustrates the basic principle. The inputs required are two consecutive gate pulses with durations respectively proportional to the two given quantities, and a third gate pulse equal to the sum of the other two. The output is a number of sawtooth pulses proportional to the product or ratio of the consecutive pulses.

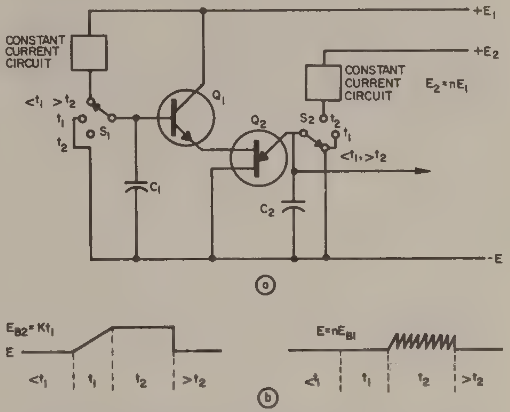

+E₁
+E₂
CONSTANT CURRENT CIRCUIT
E₂=nE₁
<t₁ >t₂
t₁
t₂
Q₁
Q₂
E_B2
E_E
<t₁,>t₂
CONSTANT CURRENT CIRCUIT
C1
C2
-E
a
E
E_B2
(E₁-Kt₁)
0
E_E
E=n(E₁-Kt₁)
b

1. **Multiplier/divider circuit** (a) operates as shown in the timing diagram (b).

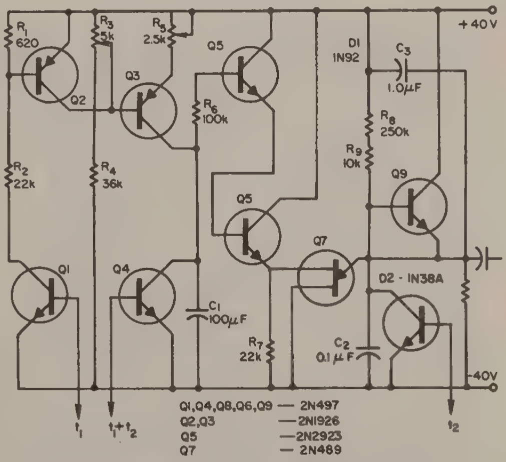
During the quiescent period ($<t_1$, $>t_2$), capacitor C_1 is connected to the $+E_1$ line, and capacitor C_2 is grounded. During interval t_1, C_1 is grounded through a constant-current circuit, so that its voltage drops linearly; at the end of interval t_1, the residual voltage on C_1 is equal to E_1 less a voltage proportional to t_1. During interval t_2, C_1 is floating; C_2 is connected through a constant-current circuit to voltage $+E_2$ equal to nE_1, where n is the intrinsic standoff ratio of the UJT. The UJT then operates as a relaxation oscillator during t_2, and the number of sawtooth pulses is proportional to the duration of t_2.

The number of pulses is inversely proportional to V_{B2}, and therefore directly proportional to the product of t_1 and t_2. By proper choice of C_1, C_2, R_3 and R_K, the number of pulses can be made equal to the product of the numerical values of the gate generating functions. Since V_E cannot go above nV_{B2}, there is no output for $t_1 = 0$, and the constant term (E_1) has no effect. There is a minimum operating voltage for the UJT, and there is a small nonlinear interval for voltages greater than the minimum.

As a divider or ratio computer (Fig. 2), the constant-current source charges C_1 during interval t_1. The number of pulses is then inversely proportional to t_1 and directly proportional to t_2, and is therefore proportional to the ratio t_2/t_1.


+E₁
+E₂
CONSTANT CURRENT CIRCUIT
CONSTANT CURRENT CIRCUIT
E₂=nE₁
<t₁ >t₂
t₁
t₂
S₁
S2
Q₁
Q₂
<t₁,>t₂
C₁
C₂
-E
a
E_B2=Kt₁
E
E=nE_B1
<t₁
t₁
t₂
>t₂
b

2. **Ratio computer circuit** is used to determine ratio of t_2:t_1, which is proportional to the number of input pulses.


R₁ 620
R₃ 5k
R₅ 2.5k
Q2
Q3
Q5
R₆ 100k
D1 IN92
C₃ 1.0μF
R₈ 250k
R₉ 10k
Q9
+40V
R₂ 22k
R₄ 36k
Q5
Q7
Q1
Q4
C1 100μF
R₇ 22k
C₂ 0.1μF
D2 - IN38A
-40V
t₁
t₁+t₂
t₂
Q1,Q4,Q8,Q6,Q9 — 2N497
Q2,Q3 —2N1926
Q5 —2N2923
Q7 — 2N489

3. **Length of objects passing a point** with constant, unknown velocity is determined by this circuit.

The circuit shown in Fig. 3 was developed to measure the length of objectives passing a point with constant but unknown velocity. A pulse is generated proportional to the time required for the object to cover a known distance between two points; this is t_1. A second pulse is then generated proportional to the time required for the object to pass the second point; this is t_2.
Hence:

$t_1 \propto$ *known length* (L_k)/*velocity* (V);
$t_2 \propto$ *unknown length* (L_u)/*velocity* (V).

Then:

$$t_1/t_2 = (L_k/V)/(L_u/V)$$
$$= (L_k/V)(V/L_u) = L_k/L_u.$$

The solution for L_k is:

$$L_u = L_k(t_2/t_1).$$

Charles D. Volz, Fishery Research Biologist, U.S. Department of the Interior, Seattle.

Age and Growth of Fishes

● John E. Watson, U. S. Bureau of Commercial Fisheries Biological
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A detailed demonstration that challenges the ingenuity of the instructor. The author suggests many alternatives that will encourage observation and analysis on the part of students

Introduction

For all living things the passage of time is accompanied by growth, maturity, and death. Direct observation and records give us the Biblical concept of a 70-year life span for mankind and the "living but for a day" term of the mayfly. By direct observation we can predict the return each year of perennial plants, the crop production of farmland, and the yield of beef from a unit of grazing area. But when we deal with fishes, we are largely denied the use of direct observation. For much of its natural life the fish is hidden from us. Its comings and goings are often puzzling, and life histories of fishes must be pieced together from scattered and fragmentary observations of their feeding, movements, and spawning. The fishing industry is concerned with an efficient harvest that satisfies its market; at the same time there must be a sufficient escapement of fishes to reproduce and perpetuate the stock. To obtain a sustained yield of optimum-sized fish from a stock, one must know its age structure, growth rates, capacity for replacement, and losses through natural causes. Excess catches beyond the capacity to produce will deplete the stock and deny the needs of the market. Fundamental to evaluating any fishery is one's ability to determine the age of the fishes that sustain it.

The concept of age determination of a fish by counting the number of rings on its scale is well known. The scale rings often are compared with the growth rings one sees on a freshly cut tree; it is implied that the ring count gives the age. Unfortunately, the ring counts do not always reveal true age, and it is here that the scientific method must be employed. Botanists, for example, have found that a tree can, under fluctuations in soil moisture and temperature, form as many as five rings in a year, each of which is indistinguishable from single rings formed in a normal year. Fishes, too, under environmental stress are known to add false growth rings. The haddock, for example, upon transfer from the ocean to an aquarium, has been found to add a false ring on its scales as clearly marked as a true growth ring. The study of growth and its evidence in the form of rings or zones is complex. In theory, a fish grows rapidly in summer and slowly in winter. Any hard part such as a scale, bone, or otolith (earstone) that grows in proportion

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to the body growth should reflect these alternating spurts and lags by wide and narrow growth zones. To prove the theory for a chosen species of fish, extensive sampling is required. It is first necessary to show that the hard part, say the scale, does increase in size almost in proportion to the growth of the fish. This study is done by plotting the body length of the fish against the length of the scale (Fig. 1).

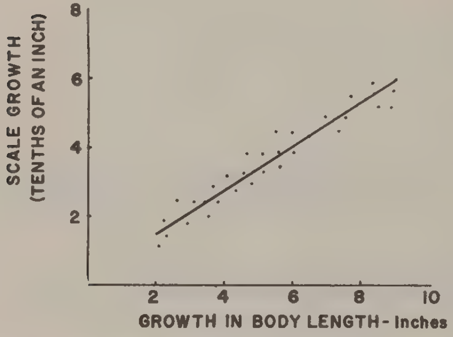

Fig. 1. Hypothetical example of a fish whose scales and body grow in direct proportion to each other.

The second step is to show that the younger fishes tend to cluster by length about a given value according to age. This length-frequency distribution is a reliable age-check for a *group* of young fishes if the spawning season occurs once a year during a short period of time, perhaps a month or two. The length-frequency method (often called the Petersen method when applied to fishes) is reliable for the first few years of life when the length measurements of the young fishes group themselves about a central value according to age (Fig. 2). If a series of samples is taken in monthly units during the growing season, it is possible to plot the length-frequency curves and watch the successive age modes "move" across the graph paper. If the formation of zones upon the scales is in step with the age modes, one can consider that he has good proof that the zone markings are annual. A logical, but time-consuming and technically difficult, proof can be established by holding fish in a large aquarium and sampling them at successive intervals to show the addition of growth zones to the scales or other hard parts. Still another proof may be obtained by removing a few scales from a living fish, marking it in some manner, releasing it into the natural environment, and recapturing it at a later date to determine how the passage of time has affected the sculpturing of the scale. When using the aquarium or marking methods one must ascertain whether the shock of marking or transferral to the aquarium causes a false mark to appear on the scale.

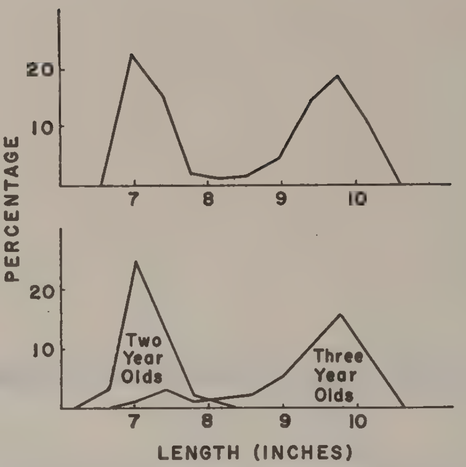

Fig. 2. Verification of herring age by the length-frequency method. The size dispersion in the upper graph coincides with age shown by otolith zones in the lower graph. Note especially the overlapping lengths of the 2- and 3-year old fishes.

Sometimes, as in the herring of the northeastern United States, scales are unreadable. Then one must use some other hard part such as the otoliths to age the fish. The otoliths are organs of balance and hearing; they are formed of minerals (essentially calcium compounds) and are not bone. If one wishes to dissect out an otolith he can find it most easily by making a sagittal slice between the eyes of a fish, dividing the head into mirror images from the snout back to the first vertebra (Fig. 3). The largest otolith, called the *Sagitta,* (there are three on each side) lies in a capsule about midway between the brain and the first vertebra. Once the otolith has been located, the sagittal section may be dispensed with and a section below the plane of the eyes used for removal of the otoliths.

Other hard parts that sometimes show growth zones and that have been used for

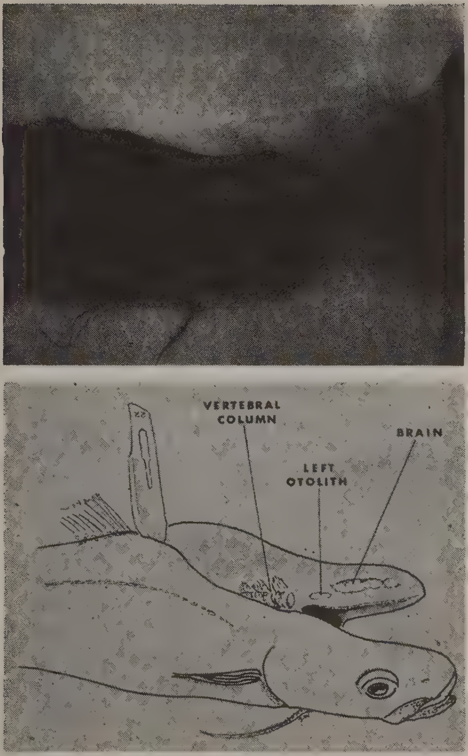

Fig. 3. Removing the otoliths of a white hake *(Urophycis tenuis)* (Above). A sagittal section through the cranium exposes the capsules containing the two large otoliths. (Below).

age determination are opercular bones and fin rays. The fin rays (spines) of the freshwater catfish have been especially useful because the fish has no scales. In most age determinations, the scale, when it is legible, is a first choice. Scales can be removed quickly from a fish at successive intervals without causing serious injury, and storage is relatively simple. But any method that is chosen must be validated with meticulous study. The validation of an aging method is obviously beyond the scope of a class assignment, and to assume that all growth zones are, by their mere existence, evidence of annual growth, would be to mislead the student.

When the method of age determination has been verified, the matter of determining average growth for a given sample is relatively easy. If a sample of goldfish has an average length of 4 inches and a weight of 6 ounces at the end of the first growing season and if the measurements are doubled at the end of the second season, one can define the average growth of that particular stock of fishes *under the environmental conditions obtaining when the measurements were made.* But to generalize upon the growth of goldfish one would need many samples taken under a range of conditions that the animal might have to meet. Growth in fishes is indeterminate; it is usually rapid in the young but it continues throughout the life of the fish even though annual growth increments may become extremely small. This growth characteristic is in sharp contrast to mammalian growth which becomes terminal, in length at least, after maturity.

The great variability of growth of a single species is largely a product of environment. The same species of fish may exhibit very different growth patterns in adjoining but dissimilar environments. Young herring, for example, show consistently better growth off the southern part of the Maine coast than they do in the north. Repeated sampling of thousands of fish during a 3-year period shows the persistence of this difference.

Once the complexities of the age problem in fishes have been discussed, a useful assignment on age and growth can be developed to show the increase in size and zonation of a hard part with an increase in fish size.

Demonstration

The chief material required is one or more fresh fish. A single fish may be used for scale demonstrations; but, preferably, a series of different-sized fish of the same species will show the differences in growth zones at different sizes. The ingenuity of the instructor and his nearness to a supply of fish will determine the specimens to be used. The members of the sunfish, perch, and bass families (Centrarchidae, Percidae, and Serranidae) are ubiquitous; they provide excellent material for scale study, but the bony cranium complicates the excision of otoliths; bone forceps are helpful in sectioning one of these "hard-headed" fishes. Whatever species is chosen, the instructor will probably wish to perform the otolith dissection as a class demonstration. For examining scales and otoliths, a binocular dissecting microscope is best. Scales should be observed in transmitted light and otoliths in reflected light. Material from fish with only a few growth zones is preferable for class study because the scale adds its growth in stair-step fashion, and the scales of old fishes are often thick, opaque, and difficult to interpret. Growth zones in otoliths, too, tend in older fishes to crowd together in slender increments that are hard to separate. The magnification and quantity of light should be just the minimum required. Small scales, as those of trout, require about 40X, whereas those of a haddock are easily studied at about 10X. The zones of a herring otolith are plainly evident at 20X; those of a silver hake can be seen with the eye unaided. Often it is desirable to moisten the scale or otolith; ordinary tap water usually suffices, and quick-acting clearing agents such as xylene should generally be avoided. Ordinarily, scales may be moistened and placed between two 1-inch by 3-inch slides for examination. Scales that have regenerated to replace missing members, and scales from the lateral line should be discarded. For study of small otoliths, I find it convenient to use a one-depression culture slide whose lower surface has been coated with waterproof black paint. The otoliths then may be completely immersed in the depression, and the black slide provides a fine background for the white (opaque) summer zones. Whatever species of fish are used, the student should be encouraged to make separate analyses and to record his observations.

Expected Results

Assuming that specimens of one species in varying sizes have been studied, the class should analyze its findings toward answering the following questions:

1. Does the size of the scale (otolith) increase approximately in proportion to the length of the fish?
2. Do the larger fish consistently show more growth zones than smaller specimens?
3. How well do different class members agree as to the number of zones they have tabulated for the specimens examined?

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GROWTH OF THE IMMATURE KING CRAB *PARALITHODES CAMTSCHATICA* (TILESIUS)

by
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Biological Laboratory, Bureau of Commercial Fisheries
Seattle, Washington, October 1965

ABSTRACT

An estimate of growth of the immature king crab of the southeastern Bering Sea is presented. From a combination of the progression of modes in successive length-frequency distributions and observations on molting, an attempt is made to identify age groups and determine age-size relationships. The growth curve derived is similar for the sexes through the first four years of life. Thereafter, female crabs grow more slowly than males and complete the immature phase in slightly less than six years. Male crabs attain sexual maturity in five years.

CONTENTS

Introduction 21
Previous Growth Studies 22
Materials and Methods 23
  Selection of Sampling Area 23
  Sampling Procedures 24
  Measurements Taken 25
  Shell Condition and Molting Stages 25
  Observations on Molting 26
Growth Description and Analysis 26
  Development and Growth of Embryonic and Larval King Crabs 26
    Embryo development and time of hatching 26
    Larval growth 27
  Size Range of Immature King Crabs 29
  Growth at Molting 31
    Molting stages 31
    Growth increment 32
    Relationship between length and width of carapace ... 33
    Changes in weight at molting 35
  Growth of Immature King Crabs at Unalaska 38
    Length-frequency distribution in all areas sampled.... 38
    Length-frequency in a single area 40
    Progression of modes and growth 41
  Growth of Immature King Crabs in Bristol Bay 42
    Length-frequency distribution 42
    Progression of modes 43
  Growth of Immature King Crabs of the Southeastern Bering Sea 44
Summary 45
Literature Cited 46
Appendix Table I 48
Appendix Table II 52

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Bull. 21, Int. North Pac. Fish. Comm., 1967.

INTRODUCTION

On the western coast of North America the common name "king crab" refers to anomuran crustaceans of the genus *Paralithodes*. Of the five known species of *Paralithodes* only three, *P. platypus* Brandt, *P. brevipes* Milne-Edwards and Lucas, and *P. camtschatica* (Tilesius), are of commercial importance[1]. The commercial species are benthonic animals inhabiting the continental shelves of the North Pacific Ocean and adjacent seas. Their distribution extends from the shores of eastern Korea northward to the Bering Strait and then south along the North American coast as far as British Columbia (Vinogradov, 1947). *P. platypus* is widely dispersed, but is most often encountered in the more northern regions. *P. brevipes*, the smallest species, is generally confined to localized areas in Asian waters. The third species, *P. camtschatica*, is most abundant south of 58° North latitude, and is the principal contributor to the king crab fisheries in both Asia and North America. This report is restricted to biological observations on *P. camtschatica*.

Exploitation of king crabs began in northern Japan and southeastern Siberia shortly before the turn of the century. The initial king crab industry was a shore-based operation, but around 1920 factoryships were developed which led to eventual expansion of this fishery into North American waters. The Japanese began to use factoryships in the southeastern Bering Sea in 1930, but this operation was discontinued in 1939. The king crab stock remained untouched until 1947 when the United States established a king crab fishery in the southeastern Bering Sea. The United States exploited these stocks alone until 1953 when the Japanese resumed a factoryship operation. Re-establishment of the Japanese fishery caused concern that the combined catch of the Japanese and United States operations might exceed the level of maximum sustained yield of the stock. Thus, in 1954 the United States undertook a joint study with Japan to determine the need for conservation measures for the king crab stock of the southeastern Bering Sea. As a part

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[1] The other two species, *P. rathbuni* (Benedict) and *P. californiensis* (Benedict), have been collected infrequently in deep water off the coast of California.

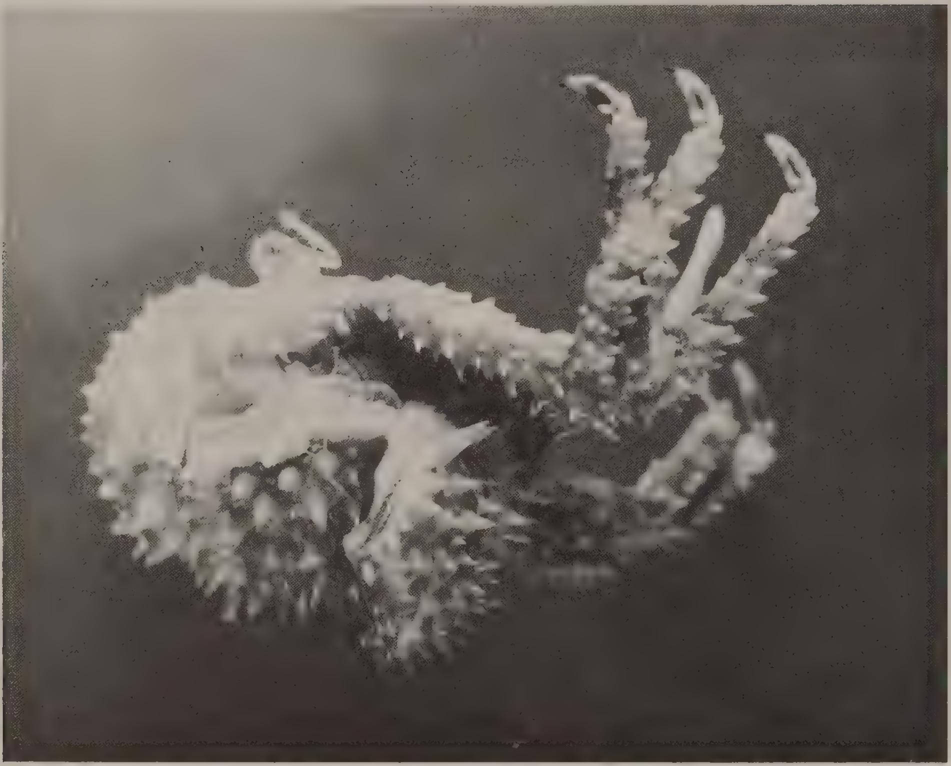

FIGURE 1. Molting immature king crab. The crab is withdrawing itself from the old shell, part of which is seen in the lower center.

of this general program to assess the need for conservation measures, the U.S. Fish and Wildlife Service initiated a study in 1958 to investigate the growth of immature king crabs.

The objectives of this report are to describe molting of immature king crabs of the southeastern Bering Sea, the changes in length and weight which accompany molting, and the resultant rate of growth. Figure 1 is a photograph of a molting immature king crab; it is included in order that the reader may gain some feeling and insight of this unusual manner of growth.

PREVIOUS GROWTH STUDIES

Published estimates of growth of immature king crabs indicate variation in growth not only between geographic areas but also within the same general locality. Examples of this variability are shown in Figure 2. The curves represent growth for both male and female crabs, and include only immature animals. The growth curves derived from reports by Wang (1937), Nakazawa (1912), Kurata (1961 b), and Marukawa (1933) are for Asiatic crabs; those presented by Powell (1960 a) and Bright *et al.* (1960) are for Gulf of Alaska king crabs. Although it is recognized that growth rates undoubtedly vary as a result of environmental and racial differences, the dissimilarities in the growth curves appear to be greater than can be ascribed entirely to these sources.

Marukawa's (1933) growth curve was derived from modes observed in width-frequency data; each mode was considered an age group. Mackay and Weymouth (1935), Kurata (1961 b), and Sato (1958) point out that several of the modes considered by Marukawa as age groups are probably instars. If these modes were deleted, Marukawa's growth curve would agree well with that of Kurata presented in Figure 2. Bright *et al.* (1960) formulated a growth curve for immature king crabs of Cook Inlet based on growth per molt and frequency of molt of crabs

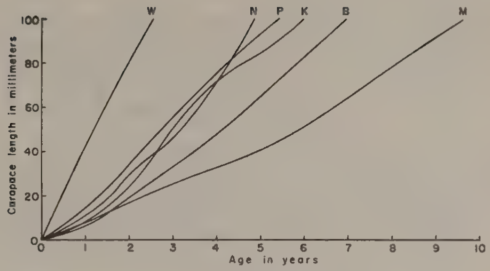

FIGURE 2. Growth curves for immature king crabs. Curves derived from Wang " W " (1937), Nakazawa " N " (1912), Kurata " K " (1961b), and Marukawa " M " (1933) are for Hokkaido king crabs. Those by Powell " P " (1960a) and Bright *et al.* " B " (1960) are for Gulf of Alaska crabs. Results by Marukawa, Wang and Nakazawa were originally expressed in terms of carapace width, but are shown here by carapace length. The conversion from width to length was made on the basis of data presented in Tables 4 and 5.

retained in live boxes. Some question always exists concerning the effect confinement may have on the frequency of molting and growth per molt. Unfortunately, Bright *et al.* did not present data by which this effect may be evaluated. Powell's (1960 a) age-length curve for immature king crabs of the Kodiak area was derived from modes in successive length-frequency distributions and growth per molt as observed from tagged crabs. As mentioned by Powell this estimate of growth is tentative because various portions of the growth curve were based on limited data. Wang (1937) estimated growth of immature king crabs from width-frequency distributions taken in 1925 and 1926 off the Kitami coast of Hokkaido. These data showed modes at carapace widths of 45 and 85 mm which Wang interpreted as age groups representing the first and second years of life. There was a semblance of a third mode at 115 mm but Wang did not consider it as an age group; he chose instead the next larger mode at 135 mm as the average size of crabs three years after hatching. Nakazawa (1912) estimated growth of Hokkaido crabs by combining data from his studies of king crab with published information on the frequency of molt and growth rate of *Homarus americanus* and *Cancer pagurus*. The growth curve for Hokkaido crabs by Kurata (1961 b) is based on growth per molt, and frequency of molt in relation to environmental temperature. As expressed by Kurata the amount of growth per molt was obtained from confined crabs, and other data utilized are fragmentary; thus the growth curve is only an approximation. Other investigators have studied size-frequency distributions (Kajita and Nakagawa, 1932) and growth per molt (Takeuchi, 1962; Sato, 1958) of immature king crabs, but the data in their reports are not sufficient to permit construction of growth curves.

MATERIALS AND METHODS

SELECTION OF SAMPLING AREA

The small size and frequent molting of immature king crabs preclude use of current methods of tagging, and there exists no known or suggested means of determining age by body structures. Thus, the only practical means of assessing growth, aside from observation of confined individuals, is to examine the progression of modes in size-frequency distributions obtained from successive samples taken in the natural environment.

The difficulty of obtaining representative samples of immature king crabs throughout their entire size range proved to be a major obstacle in determining growth by modal progression. Representative sampling of immature crabs is complicated primarily by their distribution. The larval crabs settle and tend to remain in the eulittoral zone until the carapace length reaches 40 to 50 mm. At this size the immature crabs begin to emigrate from shallow water to the sublittoral fishing grounds. As their size increases, their range of vertical movement also increases, but they are not found in quantity on the fishing grounds until they attain a length of 70 to 80 mm. Reports by Nakazawa (1912) and Takeuchi (1960), as well as surveys by the U.S. Fish and Wildlife Service, suggest that although immature crabs shorter than 60 mm are present in deeper water where fishing is conducted their distribution is not uniform either in quantity or size range. Also, the king crab is a gregarious animal, especially in early life, and solitary individuals are rarely encountered. Most immature crabs are found in groups called pods which may be composed of several hundred to several thousand individuals of similar size (Bright *et al.*, 1960; Durham, 1958; Powell, 1960 b). The shape of a pod resembles a haystack. Periodically, individuals of a pod disperse for feeding and later reassemble, often in the original location. This clustered distribution makes blind sampling with nets or trawls difficult, since most attempts will miss the crabs completely.

In May 1957, the U.S. Fish and Wildlife Service devoted 10 days to sampling the eulittoral zone along the north shore of the Alaska Peninsula. Only 85 immature king crabs were taken during this survey—77 of them in one beam trawl haul. In this same year a single beach seine haul in Akutan Bay in the Fox Islands took over 200 immature crabs. Another seine haul in shallow water near Unalaska Island in the

Aleutian chain provided an additional 30 immature crabs. Because of the difficulty of obtaining sufficient samples from a vessel, or maintaining a shore station on the coast adjacent to the Bristol Bay fishery, it appeared that if adequate samples of immature crabs were to be collected it would be advantageous to undertake sampling from a shore-based station on one of the populated Aleutian Islands. It was recognized that crabs from the Aleutian Islands might be of a different population and subject to an environment somewhat dissimilar to that of the Bristol Bay region; still the facilities available on a populated Aleutian Island would allow periodic sampling of immature crabs throughout the year. From successive samples collected, especially samples of smaller immature crabs (2 mm to 60 mm carapace length) which inhabit the eulittoral zone, a basic estimate of growth of immature crabs could be made. As information was accumulated from annual sampling of larger immature crabs (60 mm carapace length and greater) taken on the Bristol Bay commercial fishing grounds, it was to be interpreted in terms of this basic growth estimate. Therefore, in 1958 the U.S. Fish and Wildlife Service initiated a program to assess the growth of immature king crabs inhabiting the shallow waters of Iliuliuk Bay near Unalaska, Alaska.

The Bristol Bay region is geographically defined as the area north of the Alaska Peninsula and east of Unimak Pass. The king crab fishery of this area is located in the southern half of Bristol Bay. As used in this report, " Unalaska " includes only Iliuliuk Bay and vicinity; however, these observations are probably applicable to any area on the north side of the Fox Island group. Also, " southeastern Bering Sea " includes only the continental shelf bordering the northeast coast of the Fox Islands and the southern half of Bristol Bay.

Sampling Procedures

In the summers of 1955 through 1961 the U.S. Fish and Wildlife Service conducted an offshore survey of king crabs inhabiting the Bristol Bay fishing region. Samples were collected by otter trawls fished at predesignated stations 20 miles apart. At each station all crabs caught were measured, shell condition and sex were noted, and males were tagged and released. Sampling in the Bristol Bay region was described by Weber and Miyahara (1962). The remainder of this subsection pertains to sampling at Unalaska, but methods of measurement and designations of molting stages discussed are equally applicable to samples of immature crabs from the Bristol Bay fishing region.

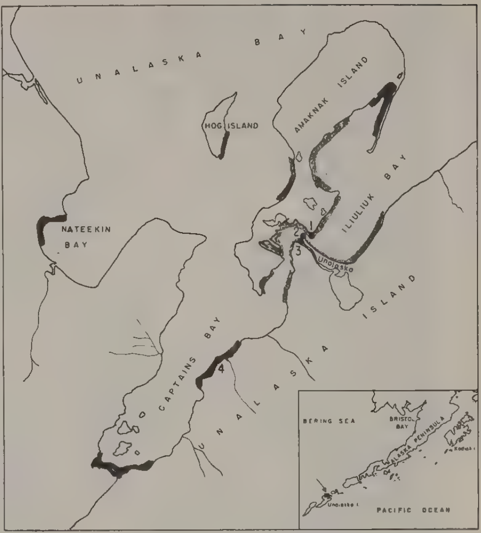

Figure 3. Area of king crab study at Unalaska. Shading indicates regions surveyed for presence of immature king crabs during each sampling period. Numbers indicate locations where the majority of immature crabs were collected.

Sampling of immature king crabs at Unalaska was carried out during four intervals from April 1958 through May 1959. Areas in which samples were collected are shown in Figure 3. Dates of sampling were as follows: (1) first period from April 22 to June 6, 1958; (2) second period from September 17 to October 1, 1958; (3) third period from February 11 to February 24, 1959; (4) fourth period from May 24 to June 2, 1959.

The most successful method of obtaining immature king crabs at Unalaska was by SCUBA diving. Other methods of capture, such as $2\frac{1}{4}$-inch (stretched mesh) tangle nets, shrimp pots, ring nets, and stomach samples of predators, yielded less than one percent of the crabs collected. During each sampling period spot checks were made at depths down to 30 feet throughout the areas indicated in Figure 3. In areas where immature crabs were found, repeated collections were made at intervals of several days, and adjacent localities were carefully surveyed.

Upon capture, king crabs were placed in holding cages until the end of the sampling period to prevent repeated captures and to observe molting. In an attempt to maintain natural conditions the cages were suspended beneath the Unalaska pier (sampling area 2 in Fig. 3)—an area found to be continuously inhabited by immature king crabs. The cages were raised daily to feed the crabs and to measure those which had molted. A supply of mussels, barnacles, and fresh fish was maintained in the holding cages.

Sex was recorded for each king crab at time of collection (females are distinguished by the asymmetrical distribution of abdominal plates and presence of abdominal pleopods).

MEASUREMENTS TAKEN

Linear measurements used in this study are length and width of the carapace measured to the nearest millimeter with vernier calipers. Carapace length (Fig. 4) is defined as the distance of a slanted line extending from the posterior median edge of the carapace to the extreme concavity of the right eye orbit; carapace width is taken as the greatest width of the carapace between marginal spines. Carapace length was recorded for each crab collected. Carapace width was recorded for all crabs collected in the first week of sampling of the first and third periods. (For immature crabs sampled in the Bristol Bay fishing region carapace width was recorded in 1957 and 1961.)

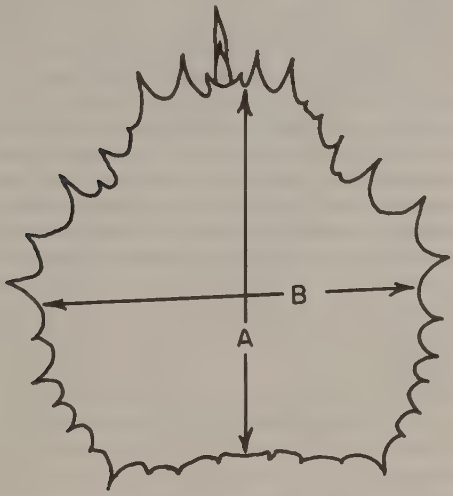

FIGURE 4. Outline of king crab carapace showing dimensions measured. A=length; B=width.

Weight was measured to the nearest gram. Prior to weighing, crabs were drained for 10 minutes to remove excess water. Crabs weighing less than 1 g were grouped by millimeter length class, weighed as a unit, and the average individual weight calculated.

SHELL CONDITION AND MOLTING STAGES

Because king crabs grow by a series of steplike increments, a crab of one size group may suddenly advance into a larger size group. Thus, the presence of two closely adjacent modes in a length-frequency distribution raises the question of whether they represent two unrelated groups or only a single group in the process of molting. The distinction between molting and non-molting crabs may be made on the basis of differences exhibited at each stage in the molting cycle.

Methods of identifying various phases of the molting cycle have been developed for some brachyuran crabs (Hiatt, 1948; Drach, 1939; Passano, 1960). These methods are based on sclerotization rates (shell hardening), physiological differences, and changes in the newly developing integument. Because we are concerned primarily with differences between groups which are and are not actively molting, an easily discernible criterion such as sclerosis is applicable. In the first sampling period king crabs were classified by carapace hardness. This character is a subjective measurement based on the degree of carapace flexibility, and is determined by application of slight manual pressure on the sides of the carapace. From observations on progressive carapace hardening of newly molted immature crabs it was found that this classification (i.e., either rigid or flexible) could be used to distinguish individuals which had molted within approximately two days prior to collection.

Color changes also have been observed prior to molting. Bright *et al.* (1960), Powell (1960 c), and Sakuda (1958) have observed a darkening of non-calcified joint areas prior to molting in both immature and adult female king crabs. These differences are evidently associated with the molting process and have also been observed in premolting brachyuran crabs (Guyselman, 1953; Drach, 1939). During the initial sampling period at Unalaska, conspicuous differences in coloration of the exoskeleton were noted, and in subsequent sampling periods coloration combined with shell hardness provided a means of classifying crabs into molting stages suitable for this study.

The molting stages used as the basis of classification in this report are as follows:

Stage 1. *Postmolt:* A period immediately following molting; weight stabilizes and linear increase terminates. Carapace is bright red and integument is flexible for one to two days after molting.

Stage 2. *Intermolt:* State of stable linear dimensions, initiated when the integument becomes rigid. During this, the lengthiest, stage of the molting cycle carapace coloration changes from a bright red to a dull red-brown. White ventral surfaces of the exoskeleton become progressively scratched and yellow as the intermolt stage progresses.

Stage 3. *Premolt:* A period of preparation for molting. The non-calcified joints of the appendages become dark red and the exoskeleton usually takes on a dark brown appearance. Terminal phases of this stage include abdominal swelling and sloughing of abdominal plates immediately prior to molting.

Stage 4. *Molt:* Actual casting of the exoskeleton accompanied by initial linear expansion and weight increase[2].

Observations on Molting

Throughout the year of study at Unalaska, molting of 317 king crabs was observed. The basic data are given in Appendix Table I. Twelve crabs had molted shortly before collection (their cast shells were found adjacent to them). The remaining observations were taken from crabs which molted in confinement.

The limited facilities at Unalaska prevented separation of confined king crabs into small groups. Thus, between daily checks, often 10 or more crabs of similar size molted in the same holding cage. To determine the individual growth increment in this situation it was necessary to identify each cast carapace correctly with the respective postmolt crab. Tagging or marking was undesirable since the effect on growth is not known. Therefore, individual differences were investigated to find means of identifying the cast shell with its former owner.

Urita (1931) studied the number and arrangement of spines on the carapace of Karafuto (southern Sakhalin) king crabs with the objective of identifying king crab stocks. He did not find a significant variation between stocks by this method, but he did find a fairly uniform arrangement of major spines and a great variation in arrangement of minor spines. The Unalaska study indicated that variation in spine arrangement may be used to identify individual immature crabs. From our observations it appears that the arrangement of minor spines, although it becomes less obvious in larger crabs, is an individual characteristic persisting throughout life. In all comparisons made, no two spine arrangements were identical. Through identification by spines, the growth increment per molt was determined for each individual by matching the cast carapace with the newly molted crab. Measurements made on the exuviae were identical with measurements made on crabs prior to molting.

GROWTH DESCRIPTION AND ANALYSIS

The following sections are a description and analysis of information derived from observations of immature king crabs in the Bristol Bay fishing region and at Unalaska. The first section treats the development and growth of the embryonic and larval crab. The most comprehensive data on egg and larval development are from Japanese investigations conducted in Bristol Bay. Duration of larval development at Unalaska is based primarily on Japanese findings. The second and third sections discuss allometric changes in the carapace with size, and growth per molt in terms of linear expansion and increase in weight. These data provide background for the analysis of advancement of modes since the observed progression of modal lengths in successive length-frequency distributions reflects changes which take place at molting. The fourth section concerns growth of immature crabs through the first three years of life. Data for this phase are from studies at Unalaska in 1958 and 1959. The fifth section presents the results of annual sampling of immature crabs by the U.S. Fish and Wildlife Service in Bristol Bay from 1957 through 1961. From these observations the growth of immature crabs from an age of four years through maturity was estimated. In the final section data on the growth of immature crabs obtained from Unalaska and Bristol Bay are combined to give a growth curve for immature crabs of the southeastern Bering Sea.

Development and Growth of Embryonic and Larval King Crabs

Embryo Development and Time of Hatching

Mature male and female king crabs undertake a characteristic annual migration pattern which appears to be similar throughout their distribution (Vinogradov, 1945; Bright *et al.*, 1960; Marukawa, 1933). Migration is in two principal stages: inshore to shallow water during the spring; offshore to deeper water at the start of summer. Inshore movement has been termed spawning migration. It generally starts in February and March, reaches a peak in April, and is completed by May. Developing eggs, which the female has been carrying for almost a year, hatch during spawning migration. The female then molts, mates, and ovulates usually within a 1–2 day interval. Studies by the Fisheries Agency of Japan (1963 a) indicate that a female crab must mate within one week after molting if ovulation and fertilization are to be successful.

Egg development has been studied and described in detail by Kajita and Nakagawa (1932) and Marukawa (1933). Briefly, the fertilized egg undergoes superficial cleavage and attains the gastrula stage 20 to 25 days after fertilization. Within 60 days the embryo enters the nauplius stage. Five months after fertilization, pre-zoeal characteristics appear. This form is retained until shortly after hatching.

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[2] Although no study was made of the changes in the integument, Stage 1 above is generally comparable to Stages A and B described by Drach (1939) and Hiatt (1948) for brachyuran crabs, and Stages 2 and 3 are similar to their C and D stages. For intermolt stages of brachyurans as cited by Passano (1960), Stage 1 above corresponds to Stages A and B, and Stages 2, 3, and 4 are Stages C, D, and E, respectively.

Time of hatching is important since it represents the base point from which age is calculated. Vinogradov (1941) found that hatching of king crab eggs takes place in March off the west coast of Kamchatka and in April in the Bay of Peter the Great. In the Nemuro region, Marukawa (1933) observed hatching from the middle of March to the beginning of May, with a peak around April 20. Nakazawa (1912) mentioned that crabs inhabiting waters adjacent to the Nemuro region hatch mainly in April, and by May 10 over 70 percent of the females carry empty egg cases.

Time of hatching in Bristol Bay may be estimated from data by Takeuchi (1962) for 1960. The Fisheries Agency of Japan (1963 a) and Niwa (1962) have made estimates for 1961 and 1962, respectively. These estimates are based on the timing of reproductive activities determined from observed changes in the condition of eggs carried by the female. Occurrence of females bearing eyed eggs, residual egg membranes, and new eggs in 1960, 1961, and 1962 are shown in Figure 5. Time of hatching extends from mid-April to mid-June; 50 percent hatching falls in mid-May. These data are consistent with similar observations by the Fisheries Agency of Japan (1956) in 1954. In 1955 and 1963 (Fisheries Agency of Japan, 1956 and 1963 b), 50 percent of the eggs hatched two to three weeks earlier.

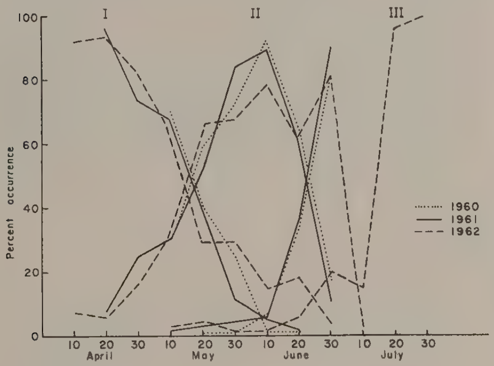

FIGURE 5. Percent occurrence, by 10-day intervals, of female king crabs bearing eyed eggs (I), empty egg cases (II), or new eggs (III) in 1960 (data from Takeuchi, 1962), 1961 (data from Fisheries Agency of Japan, 1963a), and 1962 (data from Niwa, 1962).

Time of hatching of king crabs in the vicinity of Unalaska was estimated from observations of the abundance of cast adult female shells, type of eggs carried by adult females, and time of mating activity as observed by Unalaska residents. The combined observations indicate that the peak of hatching in the Unalaska area probably occurs around mid-April. This date is several weeks earlier than in the Bristol Bay region, but the difference is not surprising if water temperature influences reproductive behavior. Sato (1958), who compiled all available data on the time of king crab spawning in Asian waters, noted a delay of one month in the spawning of northern Kuril Island crabs over crabs from the more southerly Nemuro area. As mentioned by Sato, the differences in spawning times are probably caused by differences in inshore water temperatures, which in turn might cause the period of reproductive activity to vary from one area to another and, within the same geographical area, from year to year. As will be shown in the following section, water temperatures at Unalaska are several degrees warmer than in Bristol Bay.

Larval Growth

Upon hatching the pre-zoeal larvae molt, usually within minutes, into the zoeal form. The basic zoeal structure is maintained for three consecutive molts, and on completion of the fifth molt the king crab changes into the glaucothoe larvae. The adult form is reached after the sixth molt. Morphological changes from molt to molt during larval life were described in detail by Marukawa (1933), Kajita and Nakagawa (1932), Sato and Tanaka (1949 a), and Sato (1958). Studies by Kurata (1959, 1960 a, 1960 b) and Sato and Tanaka (1949 b) considered the effect of temperature, salinity, and food supplies on growth and duration of each larval stage.

The vertical distribution of king crab larvae depends upon their developmental stage. First-stage zoeae are generally in the middle and upper water layers and as they pass through successive stages they sink to lower layers to become bottom dwellers as glaucothoe larvae. There is evidence of some diurnal vertical movement (Takeuchi, 1960), but this movement does not obscure the general downward shift as zoeae undergo successive molts.

Kurata's (1959, 1960 a, 1960 b) studies on larval and post-larval development of the king crab indicate that when adequate food is available the most important factor influencing growth is temperature. Data from Kurata (1960 a, 1961 a) show that a decrease of temperature from 10°C to 5°C doubles the length of larval life. Thus, to approximate the time at which the first adult form appears it is necessary to consider the temperature of the water which the larvae inhabit. The temperature of inshore waters of the southeastern Bering Sea during the winter is characteristically uniform from surface to bottom (U.S. Navy Hydrographic Office, 1958). In early spring a minor thermocline is usually present in the upper 10 meters. This thermocline descends rapidly, and by the end of July the surface and bottom temperatures are again nearly identical but are considerably warmer than in the winter. Isothermal conditions usually prevail throughout August and September (Dodimead *et al.*, 1963).

Since all zoeal stages, except perhaps the first when the water is essentially isothermal, are intimately associated with the middle and lower water layers, an average of bottom water temperatures should provide a reasonable indication of the temperature environment of king crab larvae. According to studies of current flow by Hebard (1959) and observations by Takeuchi (1962), bottom temperatures off Black Hill and Port Moller should be most representative of temperatures encountered by king crab larvae of the Bristol Bay region. The average inshore water temperatures at the bottom for this area of the southeastern Bering Sea for 1955 through 1961 are given in Table 1. The year-to-year variation in water temperature within this area is striking. Temperatures below 0°C were recorded in the spring of 1956 and 1959. In contrast, high bottom water temperatures of 10°C and 11°C, as recorded in August of 1938 (Favorite and Pedersen, 1959), 1939, and 1940 (Dodimead *et al.*, 1963), were uncommon during these seven years of study.

TABLE 1. Average bottom water temperatures by month off Black Hill and Port Moller, Alaska, for 1955 through 1961. Data from observations by the U.S. Fish and Wildlife Service at depths of 15 to 25 fms.

Month	Average bottom temperature (°C)	Range (°C)
May	2.1	−0.3 to 3.7
June	3.9	1.2 to 5.1
July	6.0	3.1 to 9.6
August	7.3	3.9 to 10.7

Aside from limited work by Shimizu (1936), experiments on the relation between growth of king crab larvae and water temperature have been conducted only at temperatures above 4°C. Kurata (1960 b, 1961 a) has demonstrated, however, a generally linear relationship between temperature and time required for development which may be expressed in degree days (degree days = cumulative average daily temperatures expressed in degrees centigrade). Development from hatching to the young adult form requires approximately 460 degree days (Kurata, 1961 b). On the basis of information from Kurata's estimate, a pre-zoea hatched in the Bristol Bay region in early May would attain the young adult form by mid-August.

In his 1960 study of diurnal migration of king crab zoeae in the southeastern Bering Sea, Takeuchi (1962) investigated the time of greatest abundance of each zoeal stage. In mid-May most zoeae collected were in the first stage, but a few second-stage individuals were also present. Second-stage zoeae are abundant from the end of May to mid-June. Although catches decreased to insignificant numbers by mid-June, it appeared that the majority of the second-stage zoeae were transforming into third-stage zoeae. Comparing his data with those of Marukawa (1933), Takeuchi concluded that it would take nearly one more month for the zoeae to reach the peak of the fourth stage, and an additional two weeks before a majority attained the glaucothoe stage in late July. According to Marukawa (1933) the majority of glaucothoe would metamorphose into the adult form two weeks later, or by the middle of August. This view is in agreement with the above estimate of duration of the larval stage as calculated in degree days.

Attempts to sample king crab zoeae at Unalaska were unsuccessful. Several glaucothoe larvae were collected in mid-June of 1958, but they did not appear to be numerous. The best available means of determining when the first adult form would probably appear in Unalaska waters would be by applying Kurata's (1961 b) estimate of degree days to the water temperature at Unalaska. The average monthly water temperatures at Unalaska for April through August are listed in Table 2. The average bottom temperature recorded at 6 fms for April and May 1958 was 0.3°C above the average shown in Table 2.

TABLE 2. Average water temperature at Unalaska for 1946 through 1951 (from U.S. Coast and Geodetic Survey, 1952; original data were in °F).

Month	Temperature (°C)
April	4.1
May	5.2
June	7.0
July	9.1
August	9.8

Since the peak of hatching occurs in mid-April at Unalaska, the first adult form should appear 460 degree days later, or in early July. This estimate is in agreement with Marukawa's (1933) observations of larval development in Nemuro waters. Time of hatching and water temperatures recorded by Marukawa are almost identical with those at Unalaska.

The water temperatures presented for Unalaska and Bristol Bay are not directly comparable. Bottom temperatures for Bristol Bay were taken at 15 to 25 fms, whereas observations at Unalaska were at depths not exceeding 10 fms. Limited hydrographic observations by personnel of the U.S. Fish and Wildlife Service in Bristol Bay indicate that at a comparable depth the difference of temperature between the two areas does not exceed 2°–3°C. Thus, the above estimates of mid-August for the Bristol Bay region and early July for Unalaska only generally approximate the time at which the first adult forms of king crab appear. Larvae hatched at the same time and inhabiting similar depths in both areas probably metamorphose into the adult form within a few weeks of each other.

Size Range of Immature King Crabs

The immature phase in the king crab extends from the time the larval crab metamorphoses into the adult form until sexual maturity. From rearing experiments, Kurata (1959, 1961 a), Sato and Tanaka (1949 a), and Bright *et al.* (1960) found the smallest adult form to have a carapace length of approximately 2 mm. It is interesting to note, however, that the size at sexual maturity varies from region to region. On the basis of the presence or absence of eggs carried by the females, Marukawa (1933) remarked that the average size of females at sexual maturity in the vicinity of Nemuro (northeast coast of Hokkaido) is 10–20 mm greater than off the coast of Kamchatka. Wallace *et al.* (1949) indicated that the size at which Bering Sea female crabs become oviferous ranges from 86 mm to 102 mm (carapace length), whereas in the Gulf of Alaska maturity is reached at lengths of 93–122 mm. Powell and Nickerson's (1965) observations on maturity of female crabs in the vicinity of Kodiak Island, Alaska, concur with the findings reported by Wallace *et al.* (1949) for female crabs of the Gulf of Alaska.

The percentage oviferous, by carapace length, of female crabs collected by the U.S. Fish and Wildlife Service in the southeastern Bering Sea from 1956 through 1958 is shown in Figure 6, which was plotted from data given in Table 3. These data agree with the results of Wallace *et al.* (1949) for female crabs from the southeastern Bering Sea in 1941. It should be noted that validity of figures on percentage oviferous depends on representative sampling for both mature and immature female crabs. The consequence of a disproportionally greater number of mature females, which is characteristic of these data as a result of sampling, tends to shift the oviferous ogives in Figure 6 slightly to the left. From the observed frequency of egg-carrying females it appears that the majority of female crabs in the southeastern Bering Sea mature at a carapace length between 90 mm and 100 mm.

Another method of detecting maturity is through changes in proportion of various body parts. It was

Table 3. Percentage of female king crabs oviferous, by carapace length, in southeastern Bering Sea, 1956–58.

	Sampling year								
	1956			1957			1958		
Carapace length (mm)	No eggs	With eggs	Percent with eggs	No eggs	With eggs	Percent with eggs	No eggs	With eggs	Percent with eggs
70 & less	3	0	0	21	0	0	75	0	0
75	5	0	0	45	1	2.2	28	2	6.7
80	11	2	15.4	86	0	0	86	7	7.5
85	7	2	22.2	76	2	2.6	189	69	26.7
90	22	7	24.1	46	26	36.1	225	196	46.6
95	12	5	29.4	36	58	61.7	82	258	75.9
100	7	33	82.5	20	156	88.6	19	351	94.9
105	3	39	92.9	8	175	95.6	4	550	99.3
110	0	18	100.0	2	153	98.7	3	726	99.6
115	0	43	100.0	3	184	98.4	3	617	99.5
120	0	30	100.0	2	249	99.2	1	505	99.8
125	1	10	90.9	0	233	100.0	0	345	100.0
130	0	14	100.0	0	150	100.0	1	298	99.7
135	0	23	100.0	0	85	100.0	1	199	99.5
140	0	12	100.0	0	60	100.0	0	128	100.0
145 & over	0	23	100.0	0	119	100.0	0	238	100.0
Total	71	261		345	1,651		717	4,489	

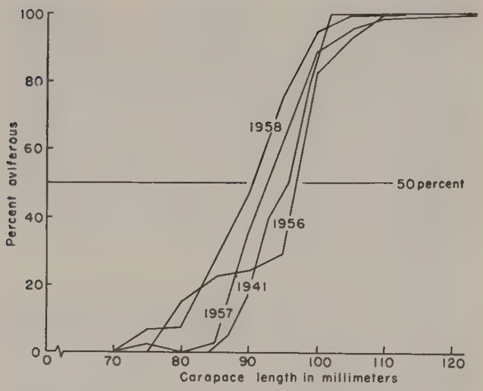

FIGURE 6. Percentage oviferous by carapace length of female king crabs collected in the southeastern Bering Sea in 1941, 1956, 1957, and 1958. The 1941 data are from Wallace *et al.* (1949).

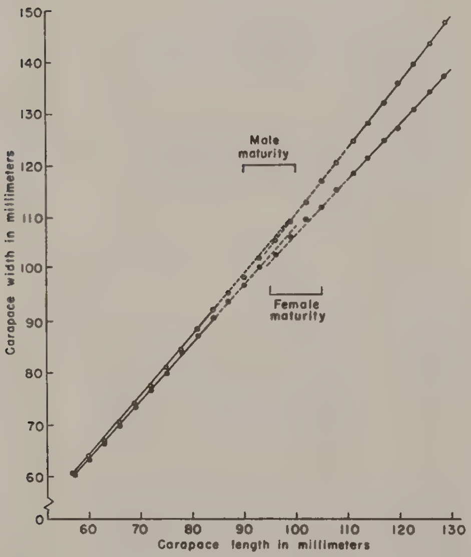

FIGURE 7. Length-width relationship for male and female king crabs of the southeastern Bering Sea. Open and closed circles represent average values by 3 mm length intervals for males and females, respectively. Solid lines were fitted by regression analysis; broken lines are extensions of the solid lines. Data on which this graph is based are given in Tables 4 and 5.

demonstrated by Marukawa (1933) and Wallace *et al.* (1949) that a change in carapace length relative to other morphological dimensions (carapace width, merus length, chela length and chela height) is a secondary sexual characteristic of female king crabs. The size at which allometric changes take place in females corresponds in general to the size at which they become oviferous. A comparison of the relative growth of carapace length and carapace width for king crabs from the southeastern Bering Sea is presented in Figure 7. A break in the length-width line for female crabs occurs at a length of 95 mm to 105

TABLE 4. Carapace length-width relationship in male and female king crabs collected in Bristol Bay in 1957 and 1961.

	Male			Female		
Carapace length (mm)	Average width by 1 mm group	Average width by 3 mm group	*N*	Average width by 1 mm group	Average width by 3 mm group	*N*
56–58		60.4	10		60.7	11
59–61		63.9	33		63.3	19
62–64		66.8	65		66.5	62
65–67		70.7	50		69.8	58
68–70		74.0	57		73.3	57
71–73		77.8	44		76.6	39
74–76		81.1	38		80.0	42
77–79		84.7	22		84.2	35
80–82		88.5	26		87.1	79
83–85		92.3	29		90.7	139
86–88		95.5	33		93.8	42
89–91		98.3	43		97.0	46
92–94		102.2	44		100.3	47
95–97		105.7	43		103.2	38
98–100		109.4	44		106.4	40
101–103		112.8	46		109.5	43
104–106		116.9	50		112.0	43
107–109		120.4	51		115.3	38
110	122.9	124.2	171	117.5	118.5	34
111	124.6		132	118.2		29
112	125.5		144	120.2		31
113	126.9	128.1	152	120.4	121.4	40
114	127.9		199	122.3		37
115	129.2		203	121.5		29
116	139.7	131.8	189	123.2	124.8	26
117	131.6		194	125.3		24
118	133.1		179	126.0		26
119	134.6	135.8	170	126.3	127.2	33
120	135.9		198	127.7		23
121	136.9		152	127.9		18
122	138.1	139.5	174	129.5	130.5	28
123	139.4		182	130.5		28
124	140.9		179	131.8		19
125	142.1	143.3	198	133.3	134.2	10
126	143.3		171	132.8		8
127	144.8		169	135.4		18
128	145.9	147.4	171	136.3	136.9	22
129	147.7		147	137.4		17
130	148.9		153	137.4		15

mm. A change in ratio of carapace length to width for males is not as evident as in females, but a slight flection appears at 90 mm to 100 mm (carapace length). Wallace *et al.* (1949) found that for male crabs of the southeastern Bering Sea a change in the relative growth of merus and chela dimensions occurred at approximately 100 mm (carapace length). Also, from histological examination of the relative degree of proliferation of cells lining the ductus deferens, Wallace *et al.* (1949) tentatively concluded that the minimum length at which males from the southeastern Bering Sea become mature is between 85 mm and 90 mm.

TABLE 5. Basic statistics for relation of carapace length to carapace width of male and female king crabs collected in the Bristol Bay region in 1957 and 1961.

Sex	Size range of carapace length (mm)	*N*	Slope *b*	Intercept *a*
Female	56–85	541	1.140	−5.244
Female	110–130	515	1.070	−0.437
Male	56–85	374	1.182	−7.347
Male	110–130	21[1]	1.267	−16.334

[1] Average values by 1 mm group as given in Table 4.

On the basis of the above discussion, the size range of immature king crabs in the southeastern Bering Sea is considered to extend from 2 mm (carapace length), as the first adult form, to approximately 95 mm at maturity.

GROWTH AT MOLTING

Molting Stages

Detailed descriptions of molting activity in king crabs may be found in Bright *et al.* (1960), Marukawa (1933), Takeuchi (1960), and Sakuda (1958). A brief resume of observations recorded at Unalaska is presented below. One or two weeks prior to molting, external coloration of the exoskeleton changes from a dull red to a dark brown and spaces between the abdominal plates begin to widen slightly. These changes indicate termination of the intermolt stage and initiation of the premolt stage. Approximately three days before casting of the old shell, the abdomen begins to enlarge. The rate of abdominal distention, although initially slow, increases rapidly 12 to 18 hours before molting. Sloughing of the abdominal plates occurs immediately prior to molting. These findings are in contrast to observations by Takeuchi (1960), Powell (1960 c), and personnel of the Fisheries Agency of Japan (1963 a), who reported that abdominal swelling begins only one to six hours before molting.

Twelve king crabs (29–39 mm in length) taken at Unalaska in the first sampling period were observed to be on the verge of molting and were placed in trays of sea water. Casting of the old shell required an average of nine minutes from the moment the carapace and the abdominal plates began to separate until the last leg was free. The time for molting agrees with observations by Mihara (1936) and Marukawa (1933) for immature king crabs. Takeuchi (1960) found that time for emergence of 13 immature crabs ranged from 8 to 40 minutes, and averaged 17 minutes. Personnel of the Fisheries Agency of Japan (1963 a) measured the time for molting at three to six minutes and observed no molting that took longer than 10 minutes. As Takeuchi (1960) pointed out, the differences in times recorded for molting may arise from the use of different reference points by various investigators for the start and end of molting.

Upon completion of molting, linear measurements were made at ½-hour intervals until maximum size had been attained. The increase, as a percentage of total growth attained for one molt, is shown in Figure 8. The king crabs attained an average of 53 percent of their growth by the time they had completely withdrawn from the old exoskeleton. This value agrees closely with observations on *Cancer magister* by Cleaver (1949) and Waldron (1958), who noted that 55.3 and 60 percent, respectively, of the linear growth was accomplished by completion of molting. By the time the exuvia is completely cast the previously distended abdomen has regained its flat intermolt form. Approximately 1½ hours elapse, however, before the carapace is completely expanded. The period of postmolt expansion apparently depends on the size of the individual; it is less for crabs smaller than those

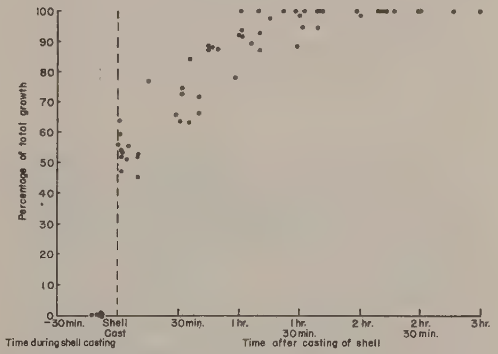

FIGURE 8. Percentage of total growth attained for one molt at varying time intervals after molting. Data from 12 crabs 29 mm to 39 mm in carapace length prior to molting.

depicted in Figure 8 and greater for larger sizes. Sakuda (1958) reported that mature female crabs 115 mm to 141 mm in carapace length continue to expand for two days after molting.

Growth Increment

Growth increments for 317 molting king crabs are shown in Figure 9. Crabs 4 mm to 62 mm (carapace length) prior to molting show an average increase in length ranging from 23 percent at 10 mm to 27 percent at 50 mm. The three observations beyond 62 mm, though few, do not agree with the growth per molt of smaller crabs and suggest a general decline in the percentage growth to about 20 percent at a carapace length of 80 mm. As is demonstrated later through an analysis of modes in size-frequency distributions, the growth per molt for immature king crabs over 60 mm long appears to remain at a nearly constant value of about 16 mm.

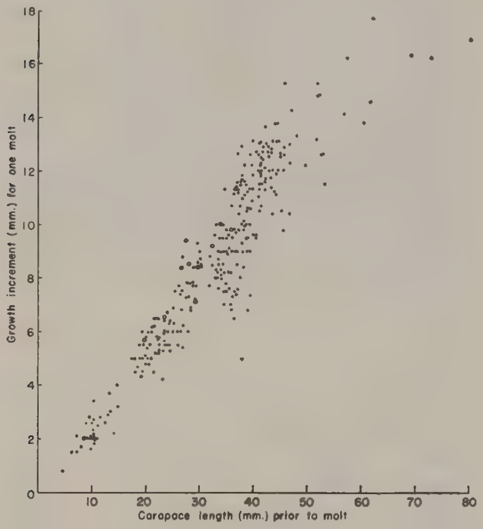

FIGURE 9. Growth increment per molt for 317 king crabs collected in the vicinity of Unalaska in 1958 and 1959. Open circles represent 12 crabs which molted prior to collection.

The literature contains a body of information on growth per molt of king crabs. The earliest observations on molting were published by Kajita and Nakagawa (1932), Mihara (1936), and Marukawa (1933), who retained immature crabs in holding cages and laboratory aquaria. Later, Sato (1958) and Bright *et al.* (1960) recorded growth per molt of immature crabs held in live boxes. Recently Takeuchi (1960) and Fisheries Agency of Japan personnel (1963 a) observed molting of immature crabs takenni Bristol Bay and held in rearing tanks aboard a factoryship.

Kurata (1961 b) reviewed the work of other investigators studying growth of immature king crabs in waters near Hokkaido and summarized their results. The combined results of the change in length at molting for Hokkaido crabs are expressed by the equation: $L_{n+1} = 0.353 + 1.086\, L_n$, where L_n is the premolt length at any given molt (n), and L_{n+1} the postmolt length. The slope (1.086) in the above equation is slightly less than that calculated from Tables 18 and 19 of Bright *et al.* (1960) for Cook Inlet crabs. The relationship at Cook Inlet, for 47 immature crabs 21 mm to 53 mm long, is expressed as: $L_{n+1}=1.162 +1.105\, L_n$. Recent studies of king crabs from the Bering Sea by Takeuchi (1960) and personnel of the Fisheries Agency of Japan (1963 a) indicate a greater growth per molt than did studies of either Kurata (1961 b) or Bright *et al.* (1960). Calculations from Table 1 of Takeuchi (1960) (observations on 31 crabs 8 mm to 17 mm long) result in the equation: $L_{n+1}= 0.012+1.183\, L_n$. Fisheries Agency of Japan (1963 a) presented results of increase per molt as: $L_{n+1}= -0.035+1.22\, L_n$, for 36 observations on crabs ranging from 8 mm to 26 mm long. None of these studies gave indication of differences between the growth per molt of male and female immature crabs, and all authors have combined the sexes in their reports.

Data from measurements of premolt and postmolt stage king crabs at Unalaska are shown in Table 6. Three observations on molting of crabs longer than 62 mm are not included since the growth per molt in the larger animals did not appear to conform linearly to the growth per molt of the smaller ones. The small values of standard error around each regression line reflect the close relationship between the two variables, L_n and L_{n+1}.

TABLE 6. Basic statistics for regression analysis of premolt (L_n) on postmolt (L_{n+1}) lengths for 314 immature king crabs 4 mm to 62 mm, premolt length.

Sex	*N*	Slope *b*	Intercept *a*	Standard error about regression (mm)
Male	148	1.278	−0.375	1.216
Female	139	1.289	−0.737	1.273
Unknown[1]	27	1.296	−0.807	0.542
All molts	314	1.284	−0.590	1.131

[1] The sex of these 27 crabs (4.3 to 34.0 mm premolt length) was not recorded.

Since the maximum difference at any one point between the regression lines for growth in length of male and female crabs does not exceed 1 mm, and values for the slopes and intercepts do not differ significantly from one another, the data were combined. The single line ($L_{n+1} = -0.590 + 1.284\,L_n$) shows an appreciably greater slope for the growth of Unalaska king crabs than those given by other investigators for crabs of other areas.

As was pointed out earlier, most of the investigators cited expressed some doubt as to the validity of observations on growth in confined animals as compared to growth under unconfined conditions. Takeuchi (1960) compared the percentage growth of crabs he held and those held by Marukawa (1933) for varying periods of time; he found no appreciable decrease in percentage growth with time in Marukawa's data, but he did state that his own observations indicated a generally decreasing trend. Takeuchi observed that the amount of growth per molt for crabs molting within one to five days after capture averaged 20 percent; for crabs held six days or longer before molting the average amount of growth attained at one molt was 16 percent—a difference of four percent.

Two assessments may be made of the effect of confinement on growth of immature king crabs collected at Unalaska. One is based on the comparison of growth at molting with duration of holding. The other compares the growth per molt of 12 immature king crabs which molted prior to collection with the growth per molt of crabs which molted in confinement.

Upon capture, crabs were placed indiscriminately into three holding cages and retained until completion of each sampling period. The longest period of holding was 46 days in the first sampling period. Maximum duration of holding for periods 2, 3, and 4 were 15, 14, and 10 days, respectively. Of the crabs which molted in confinement, more than 80 percent cast their shells within 15 days after collection. Knowing the date sampling commenced we can isolate some of the effect of confinement on growth by comparison of the growth of crabs which molted within five days after the first sample was taken with those which molted at a later date. The solid circles in Figure 10 represent 42 crabs which molted within one to five days after capture. The equation for these 42 observations is: $L_{n+1} = -0.124 + 1.273\,L_n$, which is very similar to the equation for all other crabs molting in confinement ($L_{n+1} = -0.764 + 1.288\,L_n$).

The other method of assessing the effect of confinement on the amount of growth per molt is based on comparison of the growth per molt of king crabs which were collected shortly after molting with the growth per molt of crabs which molted in confinement. As mentioned previously, 12 immature crabs and their cast shells were collected shortly after they had molted. Because the carapaces of these crabs did not increase measurably after collection, molting must have occurred at least two hours prior to capture (see Figure 8). The unconfined crabs were caught near the locality where the holding cages were placed; thus environmental conditions were similar for both confined and unconfined groups. The premolt and postmolt measurements of these unconfined crabs are depicted by the open circles in Figure 10. The regression equation for these 12 individuals is: $L_{n+1} = 0.437 + 1.287\,L_n$. The 12 observations do show a consistently greater growth per molt than the confined crabs, but they are within the range of growth for confined individuals. The growth per molt of confined crabs is similar therefore to growth per molt under unconfined conditions.

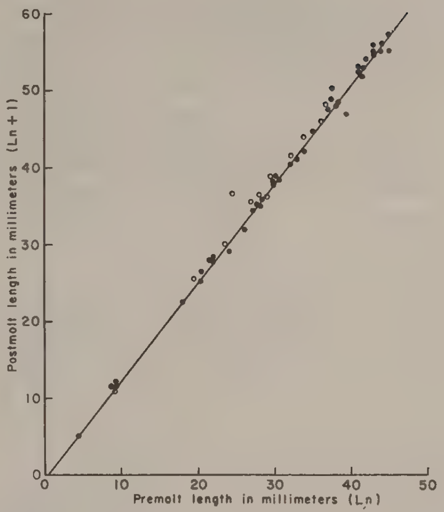

FIGURE 10. Premolt and postmolt lengths of immature king crabs collected at Unalaska. Open circles represent 12 crabs which molted before collection. Closed circles represent 42 crabs which molted one to five days after collection. The regression line ($L_{n+1} = -0.764 + 1.288\,L_n$) is for 260 crabs which molted six to 46 days after collection.

Relationship Between Length and Width of Carapace

Changes in carapace form that accompany increase in size are not only evident at maturity but during the immature stage as well. From emergence of the first young adult form to a length of 20 mm, the carapace length in both sexes is greater than the width, but beyond 20 mm the width is greater than the length. Data on length and width of male and female immature crabs collected at Unalaska are given in Table 7.

TABLE 7. Basic statistics for analysis of length on width of immature male and female king crabs collected at Unalaska. Length range, 9–64 mm.

Sex	*N*	Slope *b*	Intercept *a*	Standard error about regression (mm)
Male	360	1.082	−1.439	1.302
Female	172	1.070	−1.216	0.629
Combined sexes	532	1.080	−1.449	1.132

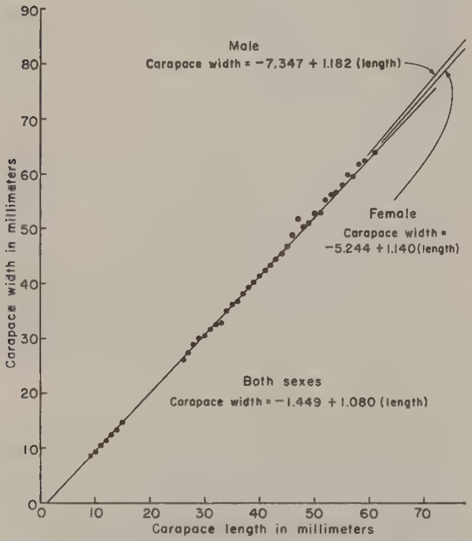

FIGURE 11. Length-width relationship of immature king crabs from Unalaska and the Bristol Bay region. Points represent average values, by 1 mm groups, of 532 Unalaska crabs. The regression line was fitted to the points by least squares. The two regression lines extending from 60 mm to 85 mm length represent length-width data from male and female crabs collected in Bristol Bay, and are identical to those presented in Figure 7.

TABLE 8. Length-width relationship for 532 immature king crabs collected at Unalaska in 1958–59.

Carapace length (mm)	Average carapace width (mm)	*N*
9	8.7	5
10	9.5	15
11	10.7	20
12	11.5	26
13	12.7	28
14	13.6	14
15	14.9	7
26	26.3	3
27	27.5	6
28	28.8	5
29	30.3	9
30	30.7	17
31	31.9	12
32	32.8	10
33	33.3	16
34	35.4	10
35	36.6	19
36	37.1	17
37	38.4	24
38	39.6	17
39	40.5	22
40	41.6	16
41	42.4	14
42	43.5	14
43	44.6	17
44	45.5	11
45	47.1	7
46	49.0	6
47	50.0	4
48	50.6	5
49	51.2	5
50	53.0	11
51	53.2	5
52	55.4	8
53	56.4	9
54	56.8	32
55	58.2	16
56	59.8	12
57	59.7	19
58	61.8	8
59	62.4	5
60	—	—
61	64.3	6

The slope and intercept values for the sexes are not significantly different. Therefore, the length-width data for male and female king crabs were combined and may be expressed by the linear equation: carapace width = −1.449 + 1.080 (carapace length). The average carapace widths by 1-mm length intervals for king crabs 9 mm to 62 mm long are plotted in Figure 11, which is based on data presented in Table 8.

In earlier discussions of changes in the length-width relationship at maturity (see Figure 7), immature king crabs from the Bristol Bay region (55–85 mm long) showed different values in the regression equation than those above. The regression lines for male and female crabs from Bristol Bay are plotted in the upper portion of Figure 11. It is interesting to note that a slight flection occurs at a length of 55 mm to 60 mm. Because the length-width data for crabs from Bristol Bay and Unalaska barely overlap, the presence of a flection point as indicated by these data alone is not conclusive. Data from other sources suggest, however, that the flection is real.

Figure 2 in Marukawa (1933) shows a change in the ratio of width to length at a width of approximately 60 mm (62 mm length), and the same is noticeable in his Figure 3, a comparison of carapace width to rostrum length. Figure 12 of the present study is based on data from Takeuchi (1960, Table 1), Bright *et al.* (1960, Tables 25 and 27), and observations in Bristol Bay by the U.S. Fish and Wildlife Serice in 1958. The regression lines are those depicted in Figure 11. The length-width ratio of immature king crabs from Unalaska is clearly similar to that of crabs of Cook Inlet and the Bristol Bay fishing region. Thus, the presence of a flection at a length of 55 mm to 60 mm does not appear to be attributable to a difference between crabs in Bristol Bay and Unalaska, but is most likely a change taking place in the length-width relationship.

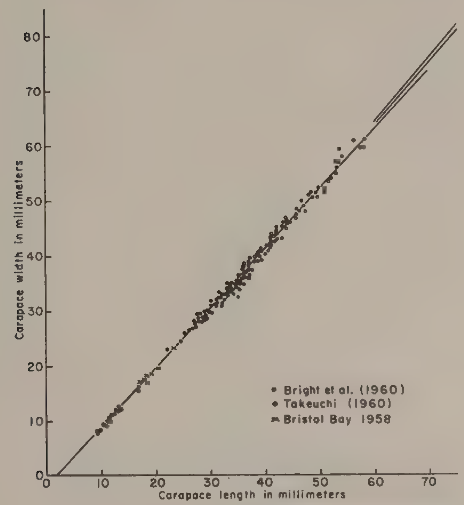

FIGURE 12. Length-width relationship of immature king crabs from the southeastern Bering Sea and the Gulf of Alaska. Data from Bright *et al.* (1960, Tables 25 and 27) for Cook Inlet crabs. Data for the Bristol Bay region from Takeuchi (1960, Table 1), and collections by the U.S. Fish and Wildlife Service in 1958. Regression lines are the same as those of Figure 11.

A change in allometric growth within the immature phase has been noticed in other decapod Crustacea. Teissier (1960) presents data on the brachyuran crab, *Maja squinado*, which indicates a prematurity change in the relative growth of the claw in relation to carapace length. This change in relative growth indicates the attainment of the prepubertal stage, at which time sexual differences begin to appear. In a discussion of various Crustacea, Teissier (1960) mentioned that morphological changes in the male are more pronounced than in the female during the prepubertal stage—female features generally remaining in accordance with previous dimensions. These remarks agree with observations on immature king crabs. Thus, the immature stage in king crabs may be divided into two length phases; the first extends from 2 mm to 60 mm, and the second (prepubertal) from 60 mm to maturity.

Changes in Weight at Molting

Rigidity of the exoskeleton prevents a change in linear dimensions except at molting, but the same is not true of body weight even though volume remains constant between molts. At time of molting, weight increases rapidly through absorption of water. The water is then replaced by soft tissue before the next molt. Since body tissue is heavier than the water absorbed, the increase in weight for any one molt lags behind the linear increase. Figure 13 shows weight in grams, by length, of 72 premolt king crabs prior to absorption of water, and 36 postmolt crabs two days after molting. The postmolt crabs consistently weigh less than premolt individuals of comparable length. Thus, calculation of the actual gain in weight per molt depends in part upon the point in the molting cycle when weight measurements are taken.

The average length-weight relationship for immature king crabs at Unalaska in the latter part of the intermolt stage is shown in Figure 14. A curve fitted

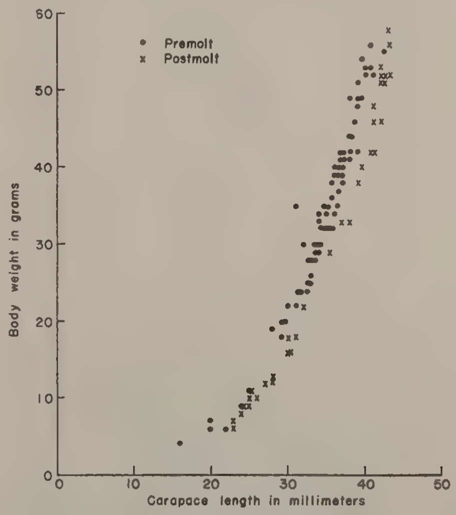

FIGURE 13. Length and weight of 72 king crabs in the premolt stage, and 36 crabs in the postmolt stage. Collections at Unalaska.

TABLE 9. Length-weight relationship for 850 immature king crabs collected at Unalaska in 1958–59.

Carapace length (mm)	Average body weight (g)	*N*
9	0.5	5
10	1.0	9
11	1.1	29
12	1.3	64
13	1.7	62
14	2.1	35
15	2.3	11
16	2.7	4
17	3.0	3
18	4.2	10
19	5.0	7
20	5.5	22
21	6.2	14
22	6.8	26
23	7.3	17
24	8.7	18
25	10.1	20
26	11.1	16
27	12.9	31
28	13.7	24
29	15.5	15
30	17.2	31
31	19.3	13
32	21.6	16
33	24.6	11
34	27.1	7
35	31.1	20
36	33.8	23
37	36.0	33
38	39.6	37
39	43.6	41
40	47.2	35
41	49.0	25
42	51.7	23
43	54.2	22
44	59.1	16
45	61.6	20
46	67.2	13
47	71.8	6
48	75.6	9
49	83.5	4
50	90.0	2

to the data represented by these points is expressed by the equation: $W=0.0012\ L^{2.937}$; where W is body weight in grams and L is carapace length in millimeters. The data from which Figure 14 was constructed are presented in Table 9.

Travis (1954) showed that body weight of the spiny lobster, *Panulirus argus*, increased an average of 10 percent just prior to molting. At molting there was a loss in body weight. This was attributed by Travis to the loss of the cast shell. The weight of *P. argus* begins to increase several hours after molting, but remains less than the premolt weight for two to four days following the molt. Such extreme fluctuations in body weight at molting were not noticed in immature king crabs. Figure 15 gives the weight change at molting of five immature crabs collected at Unalaska. The crabs were weighed at arbitrary intervals after being allowed to drain for two minutes. Weight con-

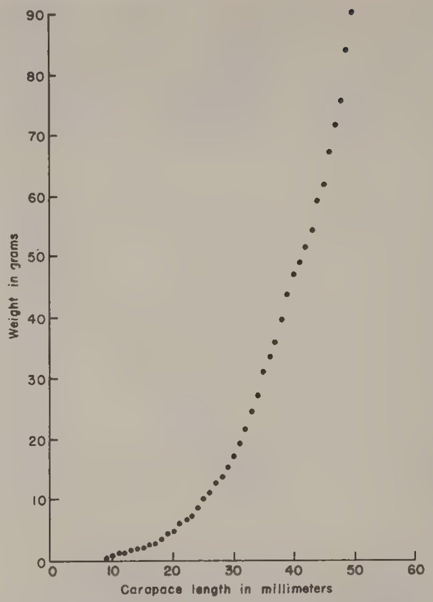

FIGURE 14. Length-weight relationship of 850 immature king crabs from 9 mm to 50 mm, carapace length. Points are average weights by 1 mm length intervals.

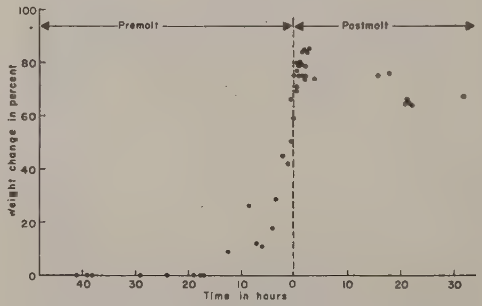

FIGURE 15. Percentage change in weight at molting of five immature king crabs 30 mm to 38 mm, premolt length. Points indicate the percentage change in weight as calculated from the premolt weight 20 or more hours prior to molting.

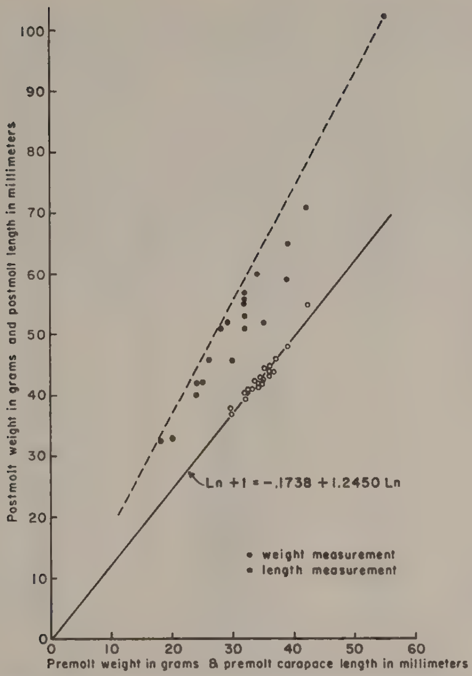

FIGURE 16. Premolt and postmolt weights and carapace lengths of 20 immature king crabs collected at Unalaska in the first sampling period. The regression (unbroken) line is based on 86 molting observations taken concurrently in the first sampling period. The broken line is the expected weight gain from intermolt stage to intermolt stage as derived from Figure 14.

tinues to increase for three to four hours after molting, and then decreases slightly during the next day. There is no evidence of loss in weight through casting of the old shell.

Figure 16 shows premolt and postmolt measurements of length and weight of 20 immature king crabs collected in the first sampling period (data are in Table 10). The average increases in length and weight for these individuals are 24.3 and 69.7 percent, respectively. The regression (unbroken) line, which represents observations of 86 molting crabs measured during the first sampling period, indicates that these 20 molting observations are representative of the average growth at this time. Weight measurements were taken prior to premolt swelling and from two to five days after molting. Because of the replacement of water by soft tissue before the next molt, the total weight gain for any one molt is slightly greater than that shown by the closed circles in Figure 16.

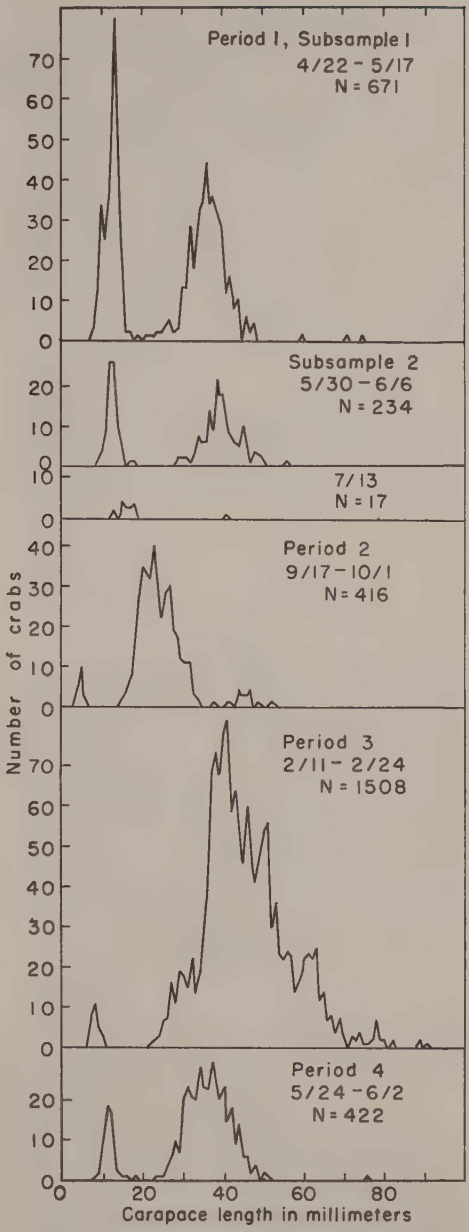

FIGURE 17. Length-frequency distribution, by sampling period, of immature king crabs collected in the vicinity of Unalaska in 1958 and 1959.

TABLE 10. Premolt and postmolt weights and carapace lengths for 20 immature king crabs collected at Unalaska in May and June of 1958.

	Premolt		Postmolt		Length increase		Weight increase	
Sex	Length (mm)	Weight (g)	Length (mm)	Weight (g)	(mm)	(%)	(g)	(%)
F	33.0	26	41.0	46	8.0	24.2	20	76.9
M	31.8	24	40.5	42	8.7	27.4	18	75.0
F	35.8	32	44.0	55	8.2	23.0	23	71.9
M	33.5	29	42.5	52	9.0	26.9	23	79.3
F	35.0	32	44.5	57	9.5	27.1	25	78.1
M	33.5	28	42.0	51	9.5	28.4	23	82.1
F	34.5	32	42.0	53	7.5	21.7	21	65.6
F	42.3	55	54.0	102	11.7	27.7	47	85.5
F	29.3	18	37.0	33	7.7	26.3	15	83.3
F	34.5	32	43.0	56	8.5	24.6	22	68.8
F	31.8	24	39.5	40	7.7	24.2	16	66.7
F	36.5	39	44.0	59	7.5	20.6	20	51.3
M	32.5	25	41.0	42	8.5	26.2	17	68.0
M	29.6	20	38.0	33	8.4	28.4	13	65.0
F	34.0	30	42.0	46	8.0	23.5	16	53.3
F	39.0	42	48.0	71	9.0	23.1	29	69.1
F	37.0	39	46.0	65	9.0	24.3	26	66.7
M	35.0	32	42.5	51	7.5	21.4	19	59.4
F	36.1	35	43.3	52	7.2	19.9	17	48.6
M	36.0	34	44.8	60	8.8	24.5	26	76.5
Average	34.5	31.4	43.0	53.3	8.5	24.3	21.9	69.7

The average expected weight gain from intermolt stage to intermolt stage is represented by the broken line. This line was calculated by determining the premolt and postmolt lengths, as based on the regression line, and the respective weights at these lengths as derived from Figure 14. The difference between the expected weight gain (broken line) and the observed weight gain (closed circles) is the amount of increase in body weight which is to be accrued before the crabs attain the next premolt stage. The difference amounts to an average of 10 percent.

GROWTH OF IMMATURE KING CRABS AT UNALASKA

Length-Frequency Distribution in all Areas Sampled

King crab zoeae hatch in the early spring. Thus, the young of one year have ordinarily grown sufficiently by the next spawning season to be easily distinguished from the succeeding brood. Overlapping of year classes apparently does not occur during the immature phase; growth may be estimated therefore from changes in the position of modes in length-frequency distributions of repeated samples from the same population.

Figure 17 shows the length-frequency distributions by sampling period for all king crabs collected during the year of study at Unalaska. The basic data from which Figure 17 and the following four figures (18–21) are derived are presented in Appendix Table II. The first period of sampling, from April to June 1958, has been divided into two sub-sampling periods, one from April 22 through May 17, and the other from May 30 through June 5. A sample of 17 individuals was taken on July 13, 1958, but this is not considered a sampling period.

More than 95 percent of the king crabs collected during the year were captured in areas 1 through 4 (Figure 3). Of the individuals taken during periods 1 and 2, 93 percent were from area 2. The two modal groups first observed in April and May shifted progressively to the right during the summer, and a new modal group appeared at about 5 mm in September.

In the third period (February 11–24, 1959) the majority of crabs were taken from pods in areas 1 and 3. These pods were composed predominantly of premolt stage individuals. Division of the length-frequency distribution of period 3, by area and molting stage, is shown in Figure 18. Position of the premolt and postmolt modes for each group are also indicated in Figure 18. In group C the small number of crabs in the postmolt stage allows some doubt as to the actual existence of modes. Their presence is partly demonstrated by the fact that the differences in length between the premolt modes at 50 mm and 61 mm and the postmolt modes at 63 mm and 78 mm are consistent with the growth per molt noted in observations on molting. Individuals of the 47 mm and 60 mm modes of group D were classified as being in the premolt stage, but those making up the 29 mm length mode were predominantly in the postmolt stage. There does not appear to be a relationship between the premolt and postmolt modes of group D.

It should be pointed out that the term postmolt as used in this section includes not only those crabs which obviously molted recently but also includes crabs in the intermolt stage. Because the difference between early and late intermolt is often difficult to detect, it was decided to limit the premolt group to those crabs which were obviously in the premolt stage. Thus, the left-hand side of the postmolt length distributions may be composed to some extent of late intermolt stage individuals prior to entering the premolt stage. These individuals should be included within the premolt group. It is realized that this method of grouping may tend to shift the postmolt modal position to the left when late intermolt individuals are numerous. For the most part, however, the postmolt modes are discrete and any distortion is of a minor nature.

Of 422 king crabs collected during period 4 (May–June 1959) all but 12 were from areas 2 and 4. Figure 19 gives the length distribution of premolt and postmolt crabs for these two areas; the distance between modes is 2–3 mm less than the average growth observed at molting.

Some modes, especially those representative of pods in period 3, appear to be groups which were not sampled continuously. It is difficult to estimate the proper placement of a mode in relation to time when it has not been observed to progress in a size-time se-

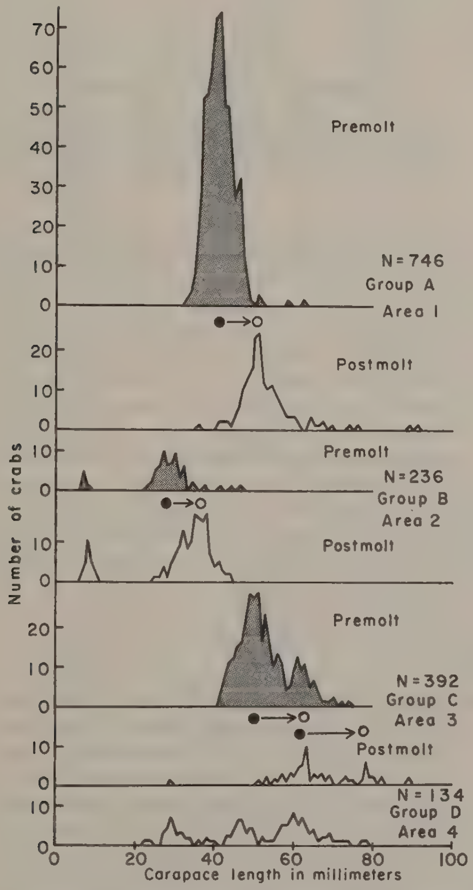

FIGURE 18. Length-frequency distribution, by sampling area (see Fig. 3) and molting stage, of immature king crabs collected in February 1959 (sampling period 3, Fig. 17); closed and open circles represent positions of premolt and postmolt modes and their advancement.

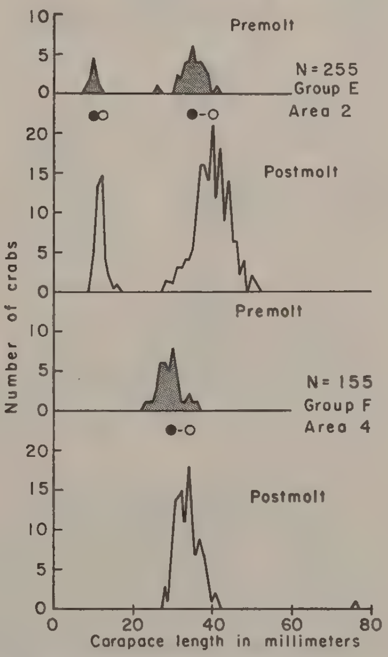

FIGURE 19. Length-frequency distribution, by molting stage, of immature king crabs collected in sampling areas 2 and 4 (see Fig. 3) during May-June 1959 (sampling period 4, Fig. 17); closed and open circles represent positions of premolt and postmolt modes and their advancement.

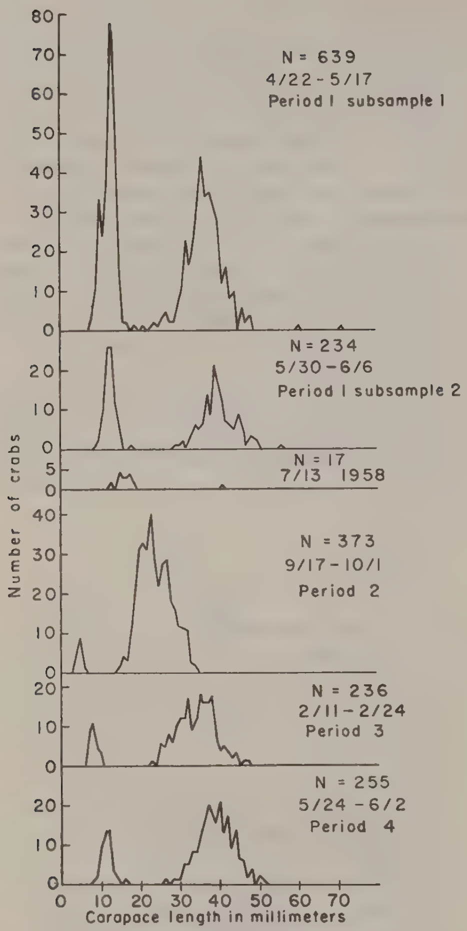

FIGURE 20. Length-frequency distribution, by sampling period, of immature king crabs collected in sampling area 2 (see Fig. 3).

quence. Since the only reliable means of determining what the modes in a sample represent is by following their progression, it is appropriate to consider first an area which was consistently sampled through the year and then to interpret data for the other groups in accordance with these results. Samples were collected in area 2 during each sampling period and in area 4 during the last three periods. Data from these samples will be used to demonstrate modal progression.

Length-Frequency in a Single Area

Figure 20 shows the length-frequency distribution of king crabs collected in area 2. Two modes are evident in the first subsample of period 1, one at 13 mm and the other at 36 mm. The smaller mode, at 13 mm, progressively shifts to the right with each successive sampling period. The mode at 5 mm that appeared in period 2 is evident at increased sizes in the following two sampling periods. In the fourth period two modes are again present in relatively the same positions as those in period 1.

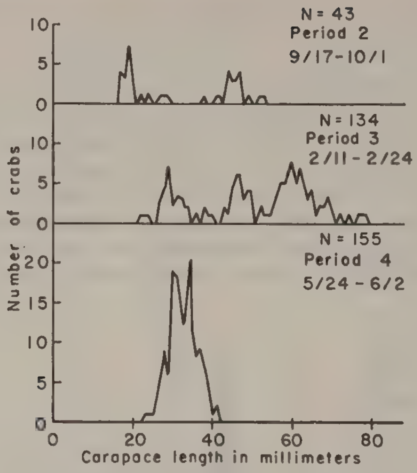

FIGURE 21. Length-frequency distribution, by sampling period, of immature king crabs collected in sampling area 4 (see Fig. 3).

Immature king crabs collected in area 4 during sampling periods 2, 3, and 4 and their size-frequency distributions are shown in Figure 21. Crabs of the 60 mm length mode of period 3 were taken only once and appear to be members of a pod moving through the area. In a survey of this area two days later, only cast shells 53 mm to 69 mm long were seen.

To establish the relation of the modes shown in Figures 20 and 21 to age it is necessary to determine a base point. As mentioned earlier, hatching of king crab zoeae in the vicinity of Unalaska occurs about mid-April, and the first young adult form is probably present by early July. As is shown in Figure 2, there is general agreement in published reports that immature crabs at the age of one year are approximately 10 mm long. Nakazawa (1912) found numerous immature crabs that averaged 10 mm long in Nemuro waters during the later part of May. From observations of the presence of king crab zoeae during May and June, Nakazawa inferred that the 10 mm individuals must have hatched one year previously. These findings agree with those of Marukawa (1933) who, through rearing experiments and collection of immature crabs in nature, concluded that 1-year-old crabs were 7 mm wide (8 mm long). On the basis of these estimates it seems reasonable to expect that a crab hatched at Unalaska in mid-April would be 2 mm long in early July and near 10 mm long one year after hatching.

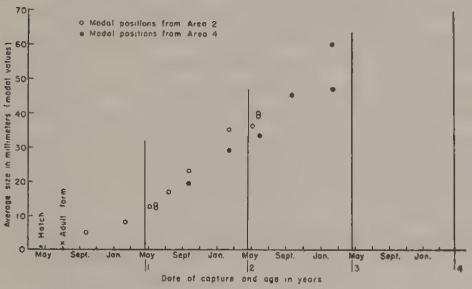

FIGURE 22. Modal values, by date of capture, of immature king crabs collected in sampling areas 2 and 4 (see Fig. 3) in 1958 and 1959.

Progression of Modes and Growth

Progression of modes is demonstrated in Figure 22, which is a plot, by date of capture, of the modal values of the one continuously present year class shown in Figure 20. This year class was first observed in early May 1958 when the modal length was 13 mm. Since king crabs near 10 mm long are probably one year old, the 13 mm crabs at Unalaska are considered to be slightly older than one year. The modal values for the year class, by date of sampling throughout the year, are shown by the open circles in Figure 22. The points extend from May at age 1 to June at age 2. In September 1958 (period 2) another distinct group of crabs 4–6 mm long was collected. This group is considered to be a younger year class whose modal values are also shown as open circles in Figure 22. These points are plotted from September of the year of hatching through June at age 1. Open circles plotted in May and June at age 2 represent the modes of larger crabs taken during the first sampling period. These modes, as plotted, complete a growth record of more than two years in duration.

With this basic relationship between size and age established, the modes representative of area 4 (Figure 21) were plotted in Figure 22 as closed circles. King crabs constituting the 60 mm mode of period 3 were regarded as less than three years old. The argument for considering these 60 mm crabs as 2-year-olds nearing three years rather than 3-year-olds is twofold: the general growth trend as depicted by modal values of smaller crabs indicates an expected size of 60 mm at age 3; a size of 60 mm at nearly age 4 would require a flection at approximately 40 mm. On the basis of data presented on allometric growth, and on the amount of growth per molt, a flection occurs at 60 mm rather than at 40 mm. Also, almost all the individuals comprising the 60 mm mode were in a premolt condition and actively molting, as is evidenced by the number of cast shells found in subsequent sampling. Results of our observations on molting show that a 60 mm crab would be about 76 mm long after molting. If this group of crabs had been available for sampling several days later, we would expect to find a modal value at 76 mm, a size more in accordance with the growth trend for crabs almost four years old.

Throughout the year of sampling, consistently large numbers of king crabs were found to be in either the premolt or postmolt stage. Therefore, if the samples had been taken two weeks earlier or later the modes observed would have been in different positions. The amount of variability expected in determining growth by modal values may be assessed by analysis of premolt and postmolt modes. Figure 23 presents the length-frequency distributions of Figure 20 divided into premolt and postmolt groups. Shell condition was not recorded in the first sampling period. Shell condition was recorded at the end of sampling period 2 on September 30, 1958, not at the time of collection.

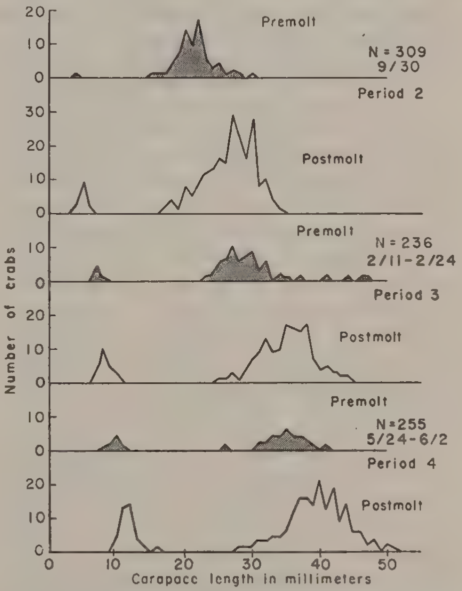

FIGURE 23. Premolt and postmolt modes, by sampling period, of immature king crabs collected in sampling area 2 (see Fig. 3).

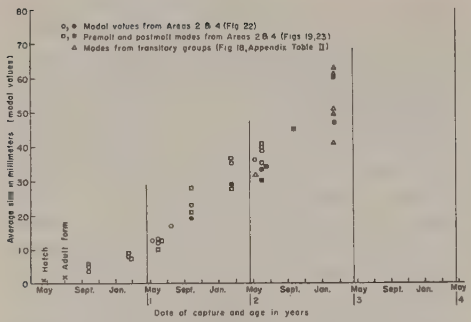

FIGURE 24. Modal values, by date of capture, of immature king crabs collected in all areas at Unalaska in 1958 and 1959.

On September 30, those crabs which had not molted while in confinement were measured, and shell condition was recorded. Data for periods 3 and 4 are taken from groups B and E of Figures 18 and 19, respectively. The premolt and postmolt modes from area 2 (Figure 23) are shown as open squares in Figure 24. The two solid squares at lengths of 30 mm and 34 mm in June at age 2 represent the premolt and postmolt values of group F (area 4) in Figure 19.

After separation of each length mode into premolt and postmolt groups, and plotting the modes of these groups on their respective sides of the unseparated length modes (as shown in Figure 24), it was possible to estimate the amount of variation in length expected in analysis of progression of modes. This variation is calculated to be approximately plus or minus 15 percent of the values of the unseparated length modes. The expected variation of 15 percent is actually less than is indicated in Figure 24, for the postmolt modes would be shifted to the right and the premolt modes to the left. This shifting would compensate for the time at which the majority of crabs would have been, or were, at a different size. The amount of shift is dependent upon molting frequency.

During the year of sampling, several groups of king crabs 30 mm to 80 mm long were not sampled continuously and are interpreted as being transient. The positioning of modes of these transient groups can only be approximated by using the previous results as a base point. In May of the first sampling period, 20 individuals were captured in one lift of a 2-inch mesh tangle net. The carapace lengths (Appendix Table II) of this group ranged from 29 mm to 35 mm, and had a mode at 32 mm. This mode is shown in Figure 24 as a triangle in May at age 2. In period 3 (February 1959) immature crabs were collected from two pods. The premolt and postmolt modes for these pods were at lengths from 41 mm to 78 mm, and are shown as groups A and C in Figure 18. For group A the premolt mode was at 41 mm and the postmolt mode at 51 mm. The combined size-frequency distribution for this group was bimodal; lengths ranged from 35 mm to 60 mm, and averaged 46 mm. In view of the size range and average length of 46 mm, the crabs represented by these premolt and postmolt modes are most reasonably classed as between age 2 and age 3; they have been plotted as triangles in Figure 24. The 50 mm premolt length mode and the 63 mm postmolt length mode of group C are also considered as being composed of crabs almost age 3. Crabs represented by the premolt mode at 61 mm (group C) have been designated as 3-year-olds, and the postmolt mode crabs as 4-year-olds. As is demonstrated later from length distributions of immature crabs collected in sampling surveys in Bristol Bay, crabs longer than 60 mm apparently molt annually. Values of the modes of the transitory groups, if plotted correctly in relation to time, extend the growth record to include the first four years of life.

A resume of results on growth of immature king crabs as determined by the Unalaska study is given in Table 11. The average lengths at the end of the first and second years of life are well defined, but the lengths at the end of the third and fourth years are not as distinct; they have been estimated in part by extrapolation of the growth trend observed for the smaller and younger crabs.

TABLE 11. Average length by age of immature king crabs in the vicinity of Unalaska, Alaska.

Age (years)	Aver. length (mm)	Range (mm)
1	11	9–14
2	35	29–41
3	60	50–67
4	80	—

GROWTH OF IMMATURE KING CRABS IN BRISTOL BAY

Length-Frequency Distribution

From 1955 through 1961 the U.S. Fish and Wildlife Service conducted an offshore survey of king crabs of the Bristol Bay fishing region. In each year except 1955 and 1956, quantities of immature crabs were collected. The length distributions of male crabs less than 120 mm long, and female crabs less than 110 mm long, are shown in Figure 25. Growth of male crabs longer than 120 mm has been reported by Weber and Miyahara (1962). Length distributions for female crabs longer than 110 mm are not given since at larger

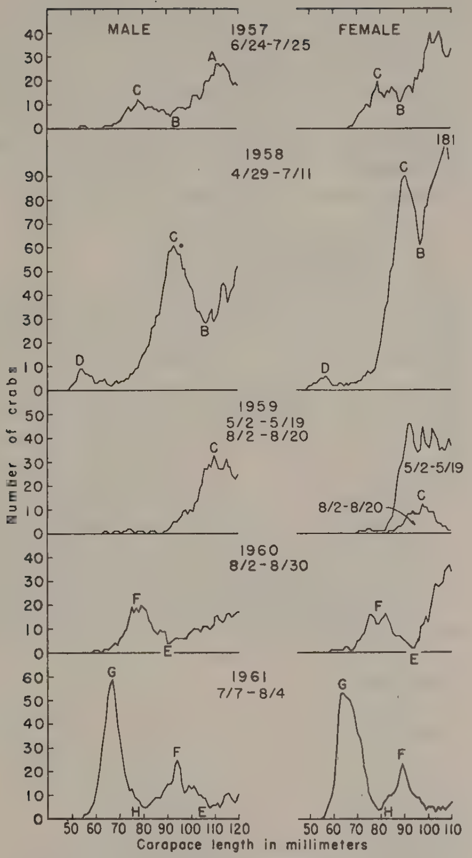

FIGURE 25. Length-frequency distributions of Bristol Bay male and female king crabs by sampling year.

sizes the reduced amount of growth per molt in females produces such overlapping of distributions of age groups that modes of individual groups become unidentifiable.

The length-frequency distributions show the presence and progression of both dominant and poorly represented groups. For convenience of discussion these groups are listed alphabetically by year of entry in the samples; the same letter identifies corresponding groups of each sex. Before the progression of these groups is considered, several points should be clarified. The king crab survey of 1959 took place in early spring and sampling of females was conducted before the majority had completed molting. Early sampling caused the length distribution of females in 1959 to be similar to the distribution of females in 1958. In August 1959 additional females were collected during a tagging program. The length-frequency distribution of females taken after molting was completed showed a mode at 98 mm. In 1958 immature crabs less than 60 mm long were numerous in the sample. In general, immature crabs do not appear on the fishing grounds until they attain 70 mm length and then are noticeable only if they constitute a particularly strong year class. Also, because of the gregarious behavior of immature crabs, a mode may represent a single trawl catch. For example, the individuals that made up mode D were collected in a single trawl haul near Port Moller. Since crabs less than 60 mm long were not collected at other locations in the 1958 survey, and mode D is not represented at an increased length in 1959, it is questionable whether the mode represented a distinct year class. The same situation applies to individuals comprising mode G in the 1961 sample. The majority of these immature crabs were taken in one haul near Port Moller. Immature crabs 60–70 mm long were encountered, however, in other trawl hauls in 1961, indicating that this mode is more likely to be representative of the average size of a dominant year class.

Progression of Modes

Figure 26 shows the positions of the dominant and poorly represented size groups of Figure 25 by their

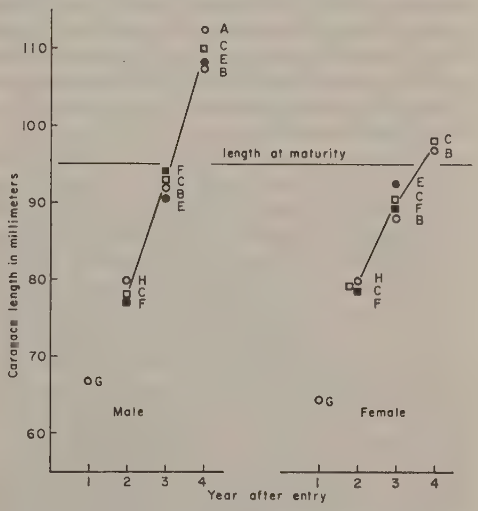

FIGURE 26. Progression of dominant and poorly represented size groups in Bristol Bay king crabs by their year of entry in the length-frequency distributions. The letters designate the groups shown in Figure 25, and the solid line shows the average progression of these groups.

year of first entry in the samples. The distance between these groups from one year to the next agrees with observations on molting at Unalaska, and results of tag returns for immature king crabs in the Gulf of Alaska. Powell (1960 a) found that tagged immature king crabs (74–91 mm long at release) in the Gulf of Alaska averaged 16 mm per molt; the same growth per molt as noted in the Unalaska studies. Advancement of modes in Bristol Bay approximates this figure; thus immature king crabs must molt only once a year after attaining a carapace length of 60 mm to 70 mm.

The position of modes in Figure 26 is not plotted by date of sampling within the season for the following reasons: Mature female king crabs molt in April and May in the Bristol Bay region; the season at which mature male crabs molt is uncertain, but it is believed to be late winter or early spring (Weber and Miyahara, 1962). Newly molted immature crabs were found infrequently, and only in early spring, in Bristol Bay. From analysis of tag returns in the Gulf of Alaska, Powell (1960 a) believes that molting of immature king crabs longer than 70 mm occurs primarily during February and March. Since immature crabs, after attaining a length of 60–70 mm, molt annually, their size remains constant from the time of molting in the early spring throughout the period of sampling. Thus, the length-frequency distributions of Bristol Bay crabs collected throughout the summer are indicative of the size taken at any time after molting is completed.

If each mode is held to represent an age group, the average annual increase in length is almost constant for male crabs in Bristol Bay. For female king crabs of Bristol Bay, a lesser rate of annual increase is evident, especially after maturity.

GROWTH OF IMMATURE KING CRABS OF THE SOUTHEASTERN BERING SEA

The 1958–59 study at Unalaska covered the growth of king crabs from time of hatching to a carapace length of 80 mm. The Bristol Bay region data included crabs of 65 mm through maturity at 95 mm. Combination of these two sets of data should give a comprehensive growth curve for immature king crabs.

Time of hatching and rate of larval development in the Bristol Bay region cause a delay of about six weeks in the time of appearance of the first adult form as compared with Unalaska. If the growth pattern of immature king crabs at Unalaska is retarded six weeks to compensate for the later development of Bristol Bay larvae, the difference at any one point in the estimated average length does not change by more than 2 or 3 mm. This difference is less than the range of variability shown by these data with the method of analysis employed.

Figure 27 shows the combined data of the Unalaska studies (Figure 24) and the modal values in Bristol Bay (Figure 26). The base point for determination of age is derived from the time of hatching as judged from the Unalaska data. Individuals comprising the Bristol Bay group at a length of 65 mm have been designated as 3-year-olds. Age-length relationships compiled from averages of the combined data are given in Table 12 and are presented graphically in Figure 28.

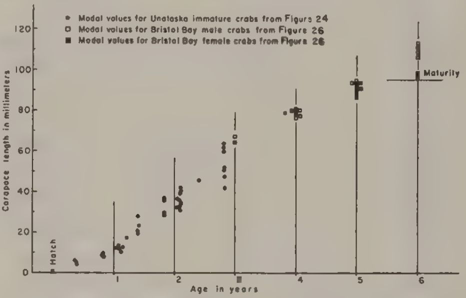

FIGURE 27. Modal values of immature king crabs in relation to age as estimated from length distributions at Unalaska and in Bristol Bay. Time of hatching is based on Unalaska data.

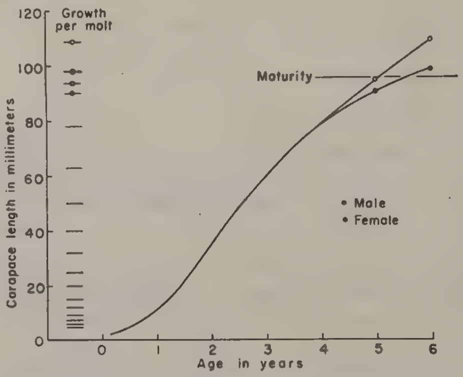

FIGURE 28. Growth curve for immature king crabs of the southeastern Bering Sea. Carapace lengths and corresponding ages are based on modal values shown in Figure 27. Cumulative growth per molt for immature crabs 5 mm and longer is shown to the left.

After an age-size relationship is determined for immature king crabs, the number of molts required to attain a given age may be calculated. Cumulative growth per molt, as determined from molting observations at Unalaska and length distributions in Bristol

TABLE 12. Average length by age of immature king crabs of southeastern Bering Sea.

Age (years)	Average carapace length (mm)	
	Male	Female
1	11	11
2	35	35
3	60	60
4	78	78
5	94	90
6	109	98

Bay, is shown to the left in Figure 28. From the first adult form to the end of the first year of life at a length of 11 mm a crab undergoes approximately 11 molts. From the end of the first year to the end of the third year immature crabs molt eight additional times, and thereafter they molt only once a year. For male crabs 80 mm and longer, the growth per molt remains nearly constant. For female crabs growth per molt decreases with increase in size.

Data presented here indicate that the immature stage of the king crab is completed at age 5 in the male and at 5½ years in the female. Growth in the first three years of life is based on Unalaska data, and for the last three years mainly on Bristol Bay data. At the junction of these two growth records (60 mm carapace length) there is a flection. An attempt has been made to explain the existence of this flection on the basis that immature crabs enter the prepubertal phase at this size. It has been demonstrated that changes in allometric growth and growth per molt occur at a length of approximately 60 mm, and one may expect these changes to be expressed in the growth curve. The possibility certainly exists, however, that two different rates of growth are involved. If the growth curve below 60 mm length were extrapolated following the growth trend as depicted by Unalaska crabs, maturity in males would occur at slightly less than five years. Conversely, extrapolation of the growth curve as represented by the growth of males in Bristol Bay would give an estimate of maturity of six years—a difference of approximately one year.

Evidence indicates that growth of king crabs does differ from region to region. Vinogradov (1947) reported that the average weight of male king crabs caught in the Primore district (northern Sea of Japan) is 3.2 kg as compared with an average weight of 1.84 kg for male crabs taken off the west coast of Kamchatka. He stated that such a variation in weight cannot be explained by differences in fishing intensity between the two areas. Wallace *et al.* (1949) wrote that mature male and female king crabs of the southeastern Bering Sea weigh less than Gulf of Alaska crabs of the same carapace length. Also, Gulf of Alaska crabs are noticeably larger than crabs from the southeastern Bering Sea, both in maximum size attained and average size as taken by the fishery. Whether these differences in length and weight are a reflection of growth throughout life is open to conjecture. Kurata (1961 b) believed differences in size between areas to be the result of variations in environmental temperature which affect the growth of crabs throughout their life cycle.

In comparison with other growth curves for immature king crabs (Figure 2), the curve derived in this study most closely approximates that of Powell (1960 a) for Gulf of Alaska crabs. The growth curve for immature king crabs of the southeastern Bering Sea is slightly to the left of Powell's curve except during the first year of life.

SUMMARY

1. The U.S. Fish and Wildlife Service initiated a study in 1958 to determine the growth of immature king crabs of the southeastern Bering Sea. The method of determining growth was based on analysis of the progression of modes in successive length-frequency distributions. Because immature king crabs change habitat with increase in size, data were collected at two different areas within the southeastern Bering Sea. Growth of immature crabs through a length of 60 mm was studied in Iliuliuk Bay of Unalaska Island, Alaska. Growth of crabs longer than 60 mm was measured in samples from the Bristol Bay fishing region.

2. Immature king crabs in the Bristol Bay fishing region were collected by otter trawls in the summers of 1957 through 1961. All crabs taken were measured, shell condition and sex were noted, and males were tagged and released. Immature crabs at Unalaska were sampled at four equally spaced intervals between April 1958 and May 1959. Samples were collected by SCUBA diving. The crabs were measured, sexed, classified into premolt and postmolt groups on the basis of shell condition, and then held in traps to observe increases in length and weight at molting.

3. Peak of hatching in the Bristol Bay region varies from year to year, but most often falls in early May. Peak of hatching at Unalaska takes place in mid-April. Duration of larval life in Bristol Bay was calculated to be three months; the glaucothoe larvae metamorphose into the first adult form by mid-August. Because of the higher water temperature at Unalaska, appearance of the first adult form occurs in early July, or approximately six weeks earlier than in Bristol Bay.

4. Size at maturity was determined by comparison of the proportion of females with and without eggs at

various carapace lengths, and by analyzing changes in length-width relationships. Both male and female king crabs of the southeastern Bering Sea mature at approximately 95 mm, carapace length.

5. Individual characteristics evident in the arrangement of carapace spines made it possible to match correctly cast carapaces with newly molted individuals under both confined and unconfined conditions. The amount of growth per molt for confined crabs 4 mm to 60 mm long ranged from 23 percent at 10 mm to 27 percent at 50 mm. The growth of unconfined crabs 9 mm to 37 mm long was one percent greater. Immature crabs longer than 60 mm show an increase of approximately 16 mm per molt.

6. The length-width ratio for immature king crabs has a flection at approximately 60 mm, carapace length. This flection appears at the size at which immature crabs enter the prepubertal phase of their life cycle.

7. The average length-weight relationship for crabs 9 mm to 50 mm long is expressed by the equation: $W=0.0012\ L^{2.937}$, where W is the body weight in grams and L is the carapace length in millimeters. Approximately 90 percent of the total weight gain for any one molt occurs within one day after molting.

8. The progression of length modes indicates that Unalaska king crabs attain a size of 60 mm, carapace length, at age 3. Separation of each length mode into premolt and postmolt groups and plotting the modes of these groups on their respective sides of the unseparated length modes indicates that the variation in length expected in analysis of progression of modes was plus or minus 15 percent.

9. Analysis of length-frequency distributions of Bristol Bay samples indicates that immature crabs longer than 65 mm molt annually.

10. Combination of data from Unalaska and Bristol Bay gave a growth curve for the entire immature stage. A male king crab hatched in the southeastern Bering Sea in late April reaches maturity five years later. A female king crab hatched at the same time requires 5½ years to attain maturity. The growth curves for the sexes are similar up to the fourth year of life (length of 80 mm). Beyond 80 mm the amount of growth per molt in the female crab decreases, whereas in the male growth per molt remains nearly constant through maturity.

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APPENDIX TABLE I. Increase in carapace length at molting for 317 immature king crabs collected at Unalaska in 1958–59.

A. Sampling period 1. N=86
Dates of molting: 4/25–6/6, 1958.

Sex[1]	Carapace length (mm)		Growth increment
	Premolt (L_n)	Postmolt (L_{n+1})	
Un	9.0	11.6	2.6
F	33.0	43.0	10.0
Un	10.0	12.0	2.0
Un	10.0	12.0	2.0
Un	11.0	13.0	2.0
Un	11.0	13.0	2.0
Un*	34.0	44.0	10.0
Un*	9.0	11.0	2.0
Un	10.0	12.0	2.0
F	25.0	31.0	6.0
M	37.0	46.0	9.0
Un	11.0	13.5	2.5
F	34.5	41.5	7.0
M	34.0	43.0	9.0
M	35.0	44.0	9.0
F	28.0	34.0	6.0
M	34.5	43.0	8.5
F	30.0	39.0	9.0
F	35.0	44.0	9.0
Un	33.0	41.0	8.0
F	10.3	12.5	2.2
M	33.5	43.0	9.5
F	34.3	43.3	9.5
Un	11.0	13.0	2.0
M	31.8	40.5	8.7
M	35.8	44.0	8.2
Un	10.3	12.1	1.8
F	34.5	43.5	9.0
F	35.8	44.0	8.2
M	36.0	44.5	9.5
M	33.5	42.5	9.0
Un	10.5	12.5	2.0
F	35.0	44.5	9.5
M	36.0	45.0	9.0
M	33.5	42.0	8.5
F	36.8	46.5	9.7
M	28.0	35.3	7.3
F	37.0	45.5	8.5
M	35.8	42.8	7.0
Un	14.0	16.2	2.2
Un	11.5	14.3	2.8
Un	10.2	13.6	3.4
Un	10.0	12.6	2.6
Un	10.1	12.4	2.3
F	34.5	42.0	7.5
F	42.3	54.0	11.7
F	29.3	37.0	7.7
F	39.2	48.2	9.0
M	34.0	43.0	9.0
F	35.5	43.1	7.6
F	34.5	43.0	8.5
M	35.2	43.5	8.3
F	38.0	47.0	9.0
Un	10.0	12.0	2.0
F	33.3	41.6	8.3
F	31.8	39.5	7.7
F	33.5	41.1	7.6
F	34.0	42.1	8.1
F	36.5	44.0	7.5
F	34.5	42.7	8.2
Un	10.3	13.0	2.7
F	14.7	18.7	4.0
F	13.5	16.5	3.0
F	13.3	17.0	3.7
M	32.5	41.0	8.5
F	35.5	44.6	9.1
M	35.1	44.0	8.9
F	36.6	44.0	7.4
M	29.6	38.0	8.4
F	34.0	42.0	8.0
F	39.0	48.0	9.0
M	12.5	15.1	2.6
Un	9.9	11.5	1.6
F	37.0	46.0	9.0
F	40.0	49.6	9.6
M	35.0	42.5	7.5
F	34.0	42.0	8.0
M	37.5	45.5	8.0
F	38.0	43.0	5.0
M	35.0	42.8	7.8
M	39.0	45.8	6.8
F	36.0	43.3	7.3
Un	13.1	16.0	2.9
Un	9.5	11.5	2.0
F	40.5	50.0	9.5
M	36.0	44.8	8.8

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[1] F=female, M=male, Un=sex unknown, * molted prior to collection.

Appendix Table I. Continued.

B. Sampling period 2. N=62
Dates of molting: 9/17–10/1, 1958.

Sex[1]	Carapace length (mm) Premolt (L_n)	Carapace length (mm) Postmolt (L_{n+1})	Growth increment
F	21.5	28.0	6.5
Un	22.0	28.0	6.0
Un	18.0	22.5	4.5
Un	22.0	28.5	6.5
M	20.5	25.3	4.8
M	20.5	26.5	6.0
M	24.0	29.5	5.5
F	21.3	27.5	6.2
M*	19.8	25.5	5.7
F	19.5	25.0	5.5
M	24.0	30.0	6.0
M	23.5	29.5	6.0
F	25.0	30.3	5.3
F	26.0	31.5	5.5
M	21.5	27.7	6.2
M	23.8	30.2	6.4
M	22.5	29.0	6.5
M	23.8	29.3	5.5
F	23.3	29.7	6.4
F	23.0	27.2	4.2
M	24.0	29.5	5.5
M	17.5	22.5	5.0
M	18.5	23.2	4.7
M	24.2	30.5	6.3
F	23.3	29.2	5.9
M	25.2	31.5	6.3
M	21.5	25.0	4.5
F	23.5	29.5	6.0
M	23.2	28.5	5.3
M	23.8	29.8	6.0
M	19.5	24.0	4.5
M	26.0	32.0	6.0
M	22.0	27.2	5.2
M	15.0	18.2	3.2
F	24.7	31.1	6.4
M	20.0	25.1	5.1
M	22.5	28.3	5.8
M	22.3	28.0	5.7
F	21.0	26.0	5.0
F	21.3	27.5	6.2
M	20.5	26.0	5.5
M	20.2	25.0	4.8
F	20.7	26.2	5.5
M	22.0	27.8	5.8
M	21.0	26.5	5.5
M	24.0	39.7	6.7
F	18.0	23.0	5.0
M	22.0	27.2	5.2
F	24.5	29.8	5.3
F	24.0	30.0	6.0
F	19.2	23.5	4.3
M	24.0	30.0	6.0
M	19.5	24.5	5.0
M	20.0	25.8	5.8
M	20.3	25.3	5.0
F	19.0	24.5	5.5
F	19.3	25.3	6.0
M	20.3	25.7	5.4
F	22.0	27.2	5.2
F	25.0	30.5	5.5
M	19.2	24.2	5.0
Un	4.3	5.1	0.8

APPENDIX TABLE I. Continued.

C. Sampling period 3. N=151
Dates of molting: 2/11-24, 1959.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
M*	28.0	36.5	8.5
F*	29.5	38.8	9.3
F*	27.4	36.8	9.4
F*	23.5	30.0	6.5
M*	26.8	35.2	8.4
F	32.0	40.8	8.8
F	29.8	38.4	8.6
M	30.2	38.6	8.4
M	61.8	76.4	14.6
M	27.5	34.7	7.2
M	39.6	47.0	7.4
F	28.3	35.1	6.8
M	44.4	56.3	11.9
M	37.5	49.0	11.5
M	30.0	38.7	8.7
F	38.3	48.2	9.9
M	45.0	57.5	12.5
F	45.5	55.3	9.8
F	42.8	55.3	12.5
M	37.6	50.5	12.9
F	41.5	53.0	11.5
F	38.3	48.1	9.8
F	43.0	55.0	12.0
M	44.2	55.3	11.1
F	41.0	53.0	12.0
F	42.1	54.2	12.1
F	41.2	52.7	11.5
F	37.8	47.8	10.0
F	43.1	55.8	12.7
F	41.5	52.2	10.7
M	25.5	33.0	7.5
F	43.6	58.5	12.9
F	33.8	43.3	9.5
F	45.2	55.7	10.5
M	43.8	54.2	10.4
M	41.6	54.0	12.4
M	42.4	55.4	13.0
M	44.7	56.7	12.0
M	41.0	54.0	13.0
F	41.9	54.8	12.9
F	43.2	56.0	12.8
F	41.4	54.5	13.1
F	43.5	55.5	12.0
F	42.7	55.5	12.7
M	36.8	48.2	11.4
F	41.0	52.3	11.3
M	41.5	53.0	11.5
F	42.2	55.5	13.3

Sex	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
F	39.0	49.6	10.6
F	37.7	49.4	11.7
M	44.5	57.6	13.1
M	37.5	48.2	10.7
F	41.4	53.9	12.5
F	37.0	48.3	11.3
M	41.4	53.2	11.8
M	38.9	50.4	11.5
M	32.8	42.4	9.6
F	28.9	37.3	8.4
M	26.2	33.6	7.4
M	27.0	35.8	8.8
M	40.7	52.2	11.5
M	26.8	36.3	7.7
M	40.7	53.3	12.6
F	36.5	43.0	6.5
F	37.0	44.6	7.6
F	37.0	48.2	11.2
M	25.3	32.2	6.9
M	41.3	53.6	12.3
M	8.0	9.8	1.8
M	43.3	55.0	11.7
F	36.9	48.5	11.6
F	39.2	51.8	12.6
M	36.6	46.4	9.8
F	38.2	50.4	12.2
M	41.2	53.1	11.9
F	56.7	70.8	14.1
M	34.9	46.2	11.3
F	35.2	44.8	9.6
F	36.0	46.7	10.7
M	41.2	51.7	10.5
F	36.0	45.8	9.8
F	39.8	52.0	12.2
F	36.3	47.6	11.3
F	38.0	49.0	11.0
F	26.8	34.2	7.4
M	44.9	58.0	13.1
M	38.3	49.4	11.1
M	39.1	50.5	11.4
M	45.7	57.7	12.0
M	30.3	38.8	8.5
M	37.2	47.0	9.8
M	39.4	50.0	10.6
F	45.0	57.7	12.7
M	38.2	48.2	10.0
M	46.9	59.9	13.0

Continued . . .

Appendix Table I. Continued.

C. Continued.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
M	23.6	29.3	5.7
M	46.6	57.0	10.4
M	45.9	61.2	15.3
M	7.2	9.3	2.1
F	45.7	58.3	12.6
F	46.9	59.2	12.3
M	44.2	58.0	13.8
F	47.0	61.3	14.3
M	52.6	65.2	12.6
F	38.9	48.4	9.5
F	41.3	53.3	12.0
M	43.1	54.7	11.6
M	41.0	52.0	11.0
M	42.3	55.2	12.9
M	38.0	47.3	9.3
M	38.9	50.1	11.2
M	41.6	54.3	12.7
M	52.2	67.0	14.8
F	37.0	49.7	12.7
M	39.8	51.1	11.3
M	26.1	32.1	6.0
F	26.8	34.3	7.5
M	80.1	97.0	16.9
F	69.2	85.5	16.3
F	42.3	56.0	13.7
F	39.8	51.6	11.8
M	37.2	47.6	10.4
M	26.9	33.7	6.8
F	57.4	73.6	16.2
M	6.5	7.3	0.8
M	73.0	89.2	16.2
M	36.8	45.8	9.0
M	38.2	48.3	10.1
F	37.8	49.6	11.8
M	44.2	58.0	13.8
F	43.2	54.6	11.4
M	39.1	49.1	10.0
M	39.9	50.8	10.9
F	52.0	67.3	15.3
M	42.2	53.8	11.6
F	43.8	55.0	11.2
M	50.6	63.8	13.2
M	41.1	53.3	12.2
F	48.0	61.3	13.3
M	49.7	61.9	12.2
M	53.4	64.9	11.5
M	7.1	8.6	1.5
F	6.4	7.9	1.5
M	60.3	74.1	13.8
F	62.2	79.8	17.6
F	43.5	56.6	13.1
M	37.7	49.3	11.6
F	40.5	53.2	12.7
M	38.9	49.4	10.5
M	39.7	52.8	13.1
M	40.5	53.2	12.7

D. Sampling period 4. N=18
Dates of molting: 5/25-6/2, 1959.

Sex[1]	Carapace length (mm) Premolt (L_n)	Postmolt (L_{n+1})	Growth increment
F*	32.2	41.4	9.2
F*	36.8	48.1	11.3
F*	36.2	46.0	9.8
F	34.0	42.3	8.3
F	35.0	44.8	9.3
M*	29.2	36.3	7.1
M	33.3	41.5	8.2
M	27.7	35.5	7.8
M	26.3	32.0	5.7
M	9.4	11.4	2.0
F	9.7	12.5	2.8
F	28.3	36.1	7.8
F	29.7	38.1	8.4
M	29.1	36.3	7.2
F	34.4	44.4	10.0
F	33.5	42.2	8.7
F	27.0	33.2	6.2
F	38.3	46.7	8.4

Appendix Table II. Length-frequency distributions by sampling period, area of capture, and molting stage of king crabs collected in the vicinity of Unalaska in 1958–59.

	1						2			3									4					
Sampling period	4/22–5/17				5/30 –6/6	7/13	9/17–10/1			2/11–2/24									5/24–6/2					
Area sampled[1]	1	2	*	Total	2	2	2	4	Total	1		2		3		4		Total	2		4		*	Total
Molting stage	not recorded									pre	post	pre	post	pre	post	pre	post		pre	post	pre	post		
Carapace length (mm)																								
4							5		5															
5							9		9															
6							2		2															
7												4	4					8						
8		3		3								1	10					11	1					1
9		11	1	12	1								5					5	2					2
10		33		33	3								3					3	4	5				9
11		24	1	25	9														1	13			4	18
12		35	1	36	26															14			3	17
13		76	3	79	26	2														4				4
14		62		62	13															2				2
15		27		27	6	4	2		2														1	1
16		2		2		3	4		4											1				1
17		2		2	1	3	3	4	7															
18					1	4	12	3	15														1	1
19		1		1			21	7	28															
20							31	4	35															
21		1		1			33		33															
22			1	1			31	1	32							1		1						
23		1		1			40		40			1				1		2			1			1
24		2		2			28	1	29			2				1		3			1			1
25		1	1	2			22		22			5	1					6			1			1
26		3	1	4			28		28			6	1					7	1		3			4
27		5		5			29	1	30			10	3			1	2	16			6			6
28		2		2			18	1	19			6	1				4	11		1	6	3		10
29	1	2		3	2		16	1	17			7	4		1	1	6	19		1	5	1		7
30	5	7	1	13	2		12		12			9	7			1	1	18		1	8	11		20
31	2	10	1	13	2		11		11			3	9				3	15	2	3	4	14		23
32	6	23		29	1		11		11			6	13				3	22	2	3	1	15		21
33	1	17		18	3		3		3	2			9				2	13	4	4	1	11		20
34	4	24		28	7		2		2	4		2	10				2	18	4	4	2	18		28
35	1	33		34	6					8		1	17					26	6	6	1	10	1	24
36		44		44	6					22	1		16				1	40	4	11	1	7		23
37		34		34	14					52		1	15					68	4	16		9		29
38		35		35	9			1	1	54			17			1	1	73	3	16		7		26
39		31		31	21					60			7			1		68	2	14		4	1	21
40		28		28	18					72			4				1	77		21		1	1	23
41		12		12	13	1		1	1	74	2	1	5					82	1	12		2		15
42		16		16	7			1	1	50	2		3	4				59		18				18
43		8		8	6					50	2		2	8		2		64		9				9
44		10		10	5			4	4	36	1	1	2	11		1	1	53		14				14
45					10			3	3	27	3			12		4		46		6				6
46		6		6	6			3	3	32	6	1		15		6		60		6				6
47		2		2	1			4	4	14	10	1		16		6		47		2				2
48		4		4	3					4	12			22		2	1	41		4				4
49					3			1	1	1	15			28		2	2	48						

Continued . . .

Appendix Table II. Continued.

	1						2			3									4					
Sampling period	4/22–5/17				5/30 –6/6	7/13	9/17–10/1			2/11–2/24									5/24–6/2					
Area sampled[1]	1	2	*	Total	2	2	2	4	Total	1		2		3		4		Total	2		4		*	Total
Molting stage	not recorded									pre	post	pre	post	pre	post	pre	post		pre	post	pre	post		
Carapace length (mm)																								
50					2						23			27		4		54		2				2
51										3	24			28	1			56		1				1
52								1	1		12			16		1	1	30						
53								1	1		10			23	2	1		36						
54											11			13		1		25						
55											10			10	1	1		22						
56					1						7			13	1	3		24						
57											5			10	3	5		23						
58										1	3			4	1	5		14						
59											3			5	3	4	2	17						
60		1		1							3			9	2	8		22						
61											2			12	4	5		23						
62										1				9	5	7		22						
63														10	10	5		25						
64											3			5	1	3		12						
65											1			6	3	3	1	14						
66											1			3	2	1		7						
67											2			1	3	2		8						
68														1	1	2		4						
69											1			1	3	3		8						
70														2		1		3						
71		1		1																				
72														1	1	1		3						
73															2			2						
74											1			1	1		1	4						
75			1	1											1			1						
76											1							1				1		1
77															1		1	2						
78															6	1		7						
79															2			2						
80															2			2						
81																								
82															2			2						
83																								
84																								
85																								
86																								
87																								
88																								
89											1				1			2						
90																								
91											1							1						
Total	20	639	12	671	234	17	373	43	416	567	179	68	168	326	66	98	36	1,508	41	214	41	114	12	422

[1] See Figure 3. * indicates crabs were collected in areas other than 1, 2, 3, and 4.

Marking Pacific Salmon with Tetracycline Antibiotics[1]

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ABSTRACT

Diets containing tetracycline antibiotics were fed to hatchery populations of Pacific salmon. Subsequent examination of bone samples from these populations indicates that the tetracyclines are deposited permanently in the skeletal structure, are readily detectable after a period of rapid growth, and do not affect growth or survival. The most satisfactory and consistent marks were obtained by feeding 250 mg of tetracycline antibiotic per kilogram of body weight per day for 4 consecutive days.

INTRODUCTION

In the winter of 1887–88, the first hatchery-reared Pacific salmon (*Oncorhynchus* spp.) were released into the Columbia River system. From this beginning an extensive complex of salmon propagation facilities has evolved on the Pacific coast. These facilities are justified on the premise that artificial propagation aids in sustaining salmon populations. Little doubt exists that salmon hatcheries do contribute to the size of the catch and survival of the species, but the difficult problem of assessing the extent of this contribution still remains.

To assess hatchery contribution, hatchery-reared individuals must be distinguished from naturally spawned individuals. We suggested previously Weber and Ridgway, 1962) that tetracycline antibiotics may be used to mark and thus identify hatchery-reared fish. We demonstrated that in fish, antibiotics of the tetracycline series localize in areas of bone proliferation. To observe the deposited tetracycline, bone is illuminated with ultraviolet light which excites the antibiotic to fluoresce as a yellow line indicating the zone of bone calcification at the time of tetracycline administration (Fig. 1). The width of the line depends on duration of tetracycline administration and rate of bone formation; the intensity depends on dosage. Multiple lines may be formed by administration at suitably spaced time intervals.

This report describes first our method of marking Pacific salmon by oral administration of tetracycline antibiotics and the methods used in detecting the resultant mark. The successive sections concern the major objectives of our study: to determine retention time of marks, and to evaluate the effects of marking on growth and survival.

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MARKING WITH TETRACYCLINES

Background

The three main tetracyclines applied in this study are tetracycline (TC), oxytetracycline (OTC), and chlortetracycline (CTC). TC is considered the parent compound, and differs from OTC by an OH group, and from CTC by a chlorine. Two other commercially produced tetracycline homologues tested for marking quality were demethylchlortetracycline (DCTC) and N-pyrrolidinomethyl tetracycline. DCTC is similar to CTC, but lacks a methyl group; N-pyrrolidinomethyl tetracycline is TC with a methane-pyrrol ring attached.

DEPOSITION

All the tetracyclines appear similar in their property of deposition in the bone. Localization of tetracyclines in areas where calcification is taking place is believed to be the result of their ability to form complexes with the apatite surface calcium of newly forming bone tissue (Isben and Urist, 1964). Kelly and Byske (1960) concluded that, with the exception of a calcium chelate formation, the tetracyclines are deposited directly from the blood onto the bone surfaces in a chemically unaltered form. Tetracyclines do not deposit in normal cartilage and soft tissue, but do deposit in calcified cartilage of skeletal neoplasms (Milch et al., 1961) and soft tissue tumors (Johnson, 1964).

ABSORPTION AND FLUORESCENCE

Detection of tetracyclines in bone depends upon their fluorescent property. Fluorescence results when a molecule absorbs light energy which raises the molecule to an excited state. Upon return to its fundamental state the molecule emits light energy (fluorescence) — usually of a longer wavelength than the light absorbed. In aqueous solution the tetracyclines display two maximum absorption peaks in the ultraviolet range, one at 270 $m\mu$ and the other at 360 $m\mu$. Hattner and Frost (1962) reported that the 360 $m\mu$ absorption peak of TC and DCTC is shifted to 440 $m\mu$ upon deposition in human bone. We have no evidence for a similar shift by any of the tetracyclines after deposition in fish bone.

The visible yellow fluorescence of tetracycline deposited in fish bone results from ultraviolet absorption in the 360 $m\mu$ range; activation of the 270-$m\mu$ absorption peak does not produce visible fluorescence. Harris et al. (1962) noticed differences in the fluorescent spectra of OTC (yellow-green) and CTC (yellow) deposited in canine bone. In fish bone all the tetracycline fluorophores we studied were yellow except for the yellow-orange fluorophore of DCTC.

Materials and Methods

FISH

Four species of Pacific salmon (coho, *Oncorhynchus kisutch*; sockeye, *O. nerka*; chinook, *O. tshawytscha*; chum, *O. keta*) and rainbow trout (*Salmo gairdneri*) were used in our studies. At time of marking, the fish weighed 2–40 g,

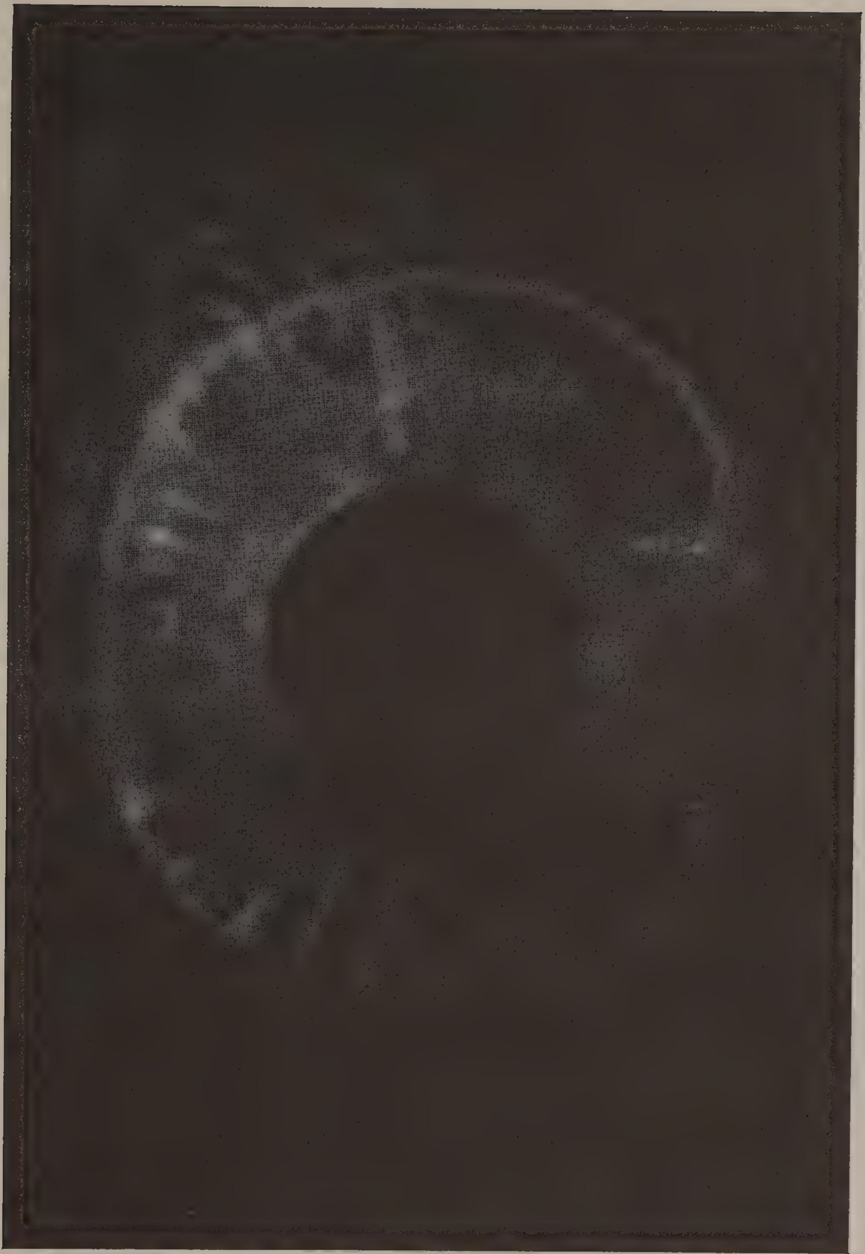

FIG. 1. Photomicrograph (35×) of a tetracycline-marked vertebral centrum from an adult sockeye salmon (*Oncorhynchus nerka*). This fish was marked with oxytetracycline as a fingerling in 1962 and recovered in 1965.

Weber and Ridgway — J. Fish. Res. Bd. Canada

but the majority of experiments were performed on fish of 5–10 g. Control groups were maintained as a check on short-term mortality and acceptability of diets.

TETRACYCLINES

Most of our studies were conducted with the following commercially available veterinary forms of CTC and OTC: water-soluble CTC and OTC with glucosamine at 25 g per pound; and CTC and OTC in feed mix at 40 and 50 g per pound respectively. Pure TC, OTC, and CTC, and human-consumption grades of DCTC and N-pyrrolidinomethyl tetracycline were used to determine if differences existed between deposited fluorophores, and in experiments where we wanted to eliminate the effects of large quantities of carrier material typical of the veterinary forms.

DIETS AND APPLICATION

The antibiotics were combined without special mixing procedures in three basic diets: commercial dry mash which was pelletized or crumbled after mixing; wet diet consisting of liver and spleen; and Oregon moist pellet as described by Hublou (1963). The proportions of antibiotic depended on the form used, dosage applied, and the percentage of body weight fed per day. To ensure complete ingestion of antibiotic, the fish were not fed for 2 days before each experiment, and the amount of food given was below the normal hatchery requirements for the prevailing water temperature and size of fish. Throughout all experiments the water temperatures were maintained between 10 and 15 C.

In force-feeding studies, gelatin capsules (No. 4) were filled with the desired quantity of antibiotic and orally administered with a 5-mm diam cork borer.

EVALUATION OF MARK

At the termination of each feeding experiment, 25 or more fish were selected at random and examined by fluorescent microscopy to determine effectiveness of marking. No analytical procedure is as sensitive as this visual technique. We assigned marking quality in relation to a standard or "good" mark resulting from intraperitoneal injection of 100 mg of OTC or CTC per kilogram of body weight. Marks resulting from feeding were divided into four categories based on the above standard: good — clear and intense; fair — clear but not intense; poor — present but neither clear nor intense; none — no mark evident.

Dose and Duration of Feeding

The results of feeding varying dosages of pure CTC in a dry pellet diet to sockeye salmon fingerlings are given in Table I. The basic relation of dose and resultant mark in this series is typical of our observations with the other antibiotics and species of fish. We found that three generally consistent factors relate dose, days fed, and marking quality. First, daily dosages are at least as important as the cumulative dose. With a cumulative dose of 1000 mg/kg, feeding less than 250 mg per day yields a large proportion of poor marks, whereas feeding 250 mg or more per day results in a majority of good marks. Second,

TABLE I. Relation of dose, days fed, and quality of mark in fingerling sockeye salmon of 5–10 g body weight. Antibiotic tested: pure CTC mixed in a dry pellet diet.

Dose per day (*mg/kg body weight*)	Consecutive days fed	Total dose (*mg/kg body weight*)	Quality of mark			
			Per cent of sample in each category			
			Good	Fair	Poor	None
25	10	250	0	12	76	12
50	5	250	0	8	60	32
50	10	500	0	44	56	0
100	10	1000	4	68	28	0
125	8	1000	10	68	22	0
200	5	1000	32	49	14	5
250	4	1000	50	50	0	0
333	3	1000	68	18	12	2
500	2	1000	60	30	0	10
500	3	1500	78	18	4	0
500	4	2000	93	7	0	0
400	5	2000	89	11	0	0
667	3	2000	79	19	1	1
1000	2	2000	55	20	10	15

there is a limit in daily dosages of antibotic above which the resultant mark is not improved; orally, this dose is 500 mg per kilogram per day (intraperitoneally, it is 100 mg per day). Third, when the dose is sufficient the percentage marked is directly related to the number of days fed. Individual daily feeding response varies within a group of fish, and 100% marking is not achieved unless feeding is continued several consecutive days. Feeding for 2 or 3 consecutive days usually gives marks of varying intensity in 85–95% of the fish, whereas feeding for 4 or 5 consecutive days gives marks of uniform intensity in 96–100% of the individuals.

A total dosage of 1 g of tetracycline antibiotic per kilogram of body weight divided into doses of at least 250 mg/kg and given over 3 or 4 consecutive days normally produces a good mark. Several additional factors, however, may improve or diminish the effectiveness of marking.

CALCIUM CONTENT OF DIET

The high oral dosage we found necessary for satisfactory marking probably indicates that fish are inefficient in absorbing tetracyclines from the gut. There is evidence that some of this inefficiency may be the result of the presence of calcium in the diet.

Calcium and other divalent and trivalent metallic cations will chelate with tetracyclines and reduce absorption of the antibiotic. This reduction was found by Donovan et al. (1962), who noted that chickens fed poultry rations containing 0.3% dietary calcium had significantly higher blood levels of antibiotic than when fed higher levels of calcium. Studies by Westgate et al. (MS, 1964) on fingerling chinook salmon indicated that TC and OTC incorporated in a low-calcium (0.25%) Oregon pellet diet produced an appreciably better mark than the same antibiotic dose fed in standard Oregon pellet (2,0% calcium).

POTENTIATORS

The introduction of a potentiator, a compound which enhances the action of another compound, has been shown to increase the blood level of tetracycline in birds and mammals (Gittinger and Wiener, 1960; Harms et al., 1963). In one set of experiments we mixed pure CTC with two common potentiators, glucosamine and terephthalic acid, and force-fed single doses of these tetracycline complexes to fingerling sockeye salmon. The intensity of deposited fluorophore definitely increased in the group given glucosamine, upgrading the mark from fair to good (Table II). Terephthalic acid, though not as effective as glucosamine, also improved the mark.

FISH SIZE

Osteogenesis in Pacific salmon and rainbow trout has advanced sufficiently for uptake of tetracycline when the yolk sac is completely absorbed (called the "button-up" stage). At this stage the ribs and vertebral plates surrounding the notochord are beginning to form, and tetracycline may be incorporated on their growing surfaces. From button-up through the fingerling stage there is an increase in the quantity of bone matrix undergoing calcification, and thus, an increase in the number of available sites for tetracycline deposition.

The consequence of increasing calcification on tetracycline deposition is observed by the upgrading of marking quality coincident with administration of similar doses of tetracycline at progressively larger sizes. Jones and Steel (MS, 1965) made multiple marks on coho salmon fingerlings of various sizes by

TABLE II. Results of force-feeding fingerling sockeye salmon (weight range 30–35 g) different single doses of CTC mixed with glucosamine and terephthalic acid (TPA).

Dose CTC (*mg/kg body weight*)	Number of fish	Dose of potentiator (*mg/kg body weight*)		Quality of mark		
		Glucosamine	TPA	Good	Fair	Poor
300	8	Control	Control	1	7	–
300	7	–	4.0	2	5	–
300	7	24.8	–	5	2	–
250	5	Control	Control	–	3	2
250	5	–	8.0	–	5	–
250	5	12.0	–	2	3	–

repeatedly feeding TC in a low-calcium Oregon pellet. TC fed at a dosage of 1 g/kg over 4 days at a count-weight of 290 per pound resulted in a poor mark, whereas the same dosage and duration of feeding at count-weights of 100, 50, and 25 per pound gave fair marks. Samples of the cleithrum from these multiple-marked fish after 7 months of oceanic life "showed 28% marked from feeding at 290 per pound, 97% from feeding at 100 per pound, and 100% from feeding at 50 and 25 per pound" (Jones, MS, 1965).

The smallest fish we marked and subsequently recovered after a period of oceanic life were chum salmon. These fish were at a count-weight of 220 per pound when fed a total dose of 2 g/kg of OTC with glucosamine mixed in a dry pellet diet given over 5 consecutive days. The marking quality was fair to good both at release in 1963 and at recovery in 1965.

TETRACYCLINES

A 300-mg/kg dose of each of the pure forms of TC, OTC, CTC, and human-consumption grades of DCTC and N-pyrrolidinomethyl tetracycline was force-fed to 10-g sockeye, coho, and chinook salmon. The resultant fluorescence of the deposited tetracyclines was of equal intensity with the exception of DCTC, which was noticeably greater. It has also been reported by Hattner and Frost (1962) that, gram for gram, DCTC deposited in mammalian bone has a more intense fluorescence than other tetracyclines.

We found DCTC identical in acceptability and lack of toxicity to the other tetracyclines, but did not conduct major feeding trials with it because this antibiotic is not available in low-cost veterinary grades. N-pyrrolidinomethyl tetracycline, which is highly soluble, did not differ in deposition or efficiency of marking from TC, OTC, and CTC.

Acceptability of Antibiotic Forms

The acceptability of diets containing antibiotics was tested on rainbow trout and sockeye and chinook salmon. In these tests the experimental and control groups were fed 3 times a day for 3 or 4 consecutive days; feeding responses of the associated control groups were excellent.

Most veterinary forms of antibiotic were accepted at high levels in the three basic diets. Diets containing up to 50% water-soluble forms of CTC and OTC with glucosamine were readily consumed by all species.

Experiments were conducted on the relation between acceptability and percentage concentration of antibiotic feed mixtures incorporated in the diet (Table III). At low concentrations commercial feed mixtures containing either CTC or OTC are acceptable. CTC in feed is acceptable to sockeye salmon and rainbow trout when it constitutes less than 40% of the diet, but chinook salmon tend to reject CTC feed mixtures when it exceeds 20% of the diet. Diets containing OTC in feed gave varied results; most experiments indicated a low level of acceptance. Other experiments also indicated low acceptance but they were terminated after 2 days. They are not included here because unacceptable antibiotic forms are usually accepted during the first and often

TABLE III. Results of experiments on acceptability of CTC and OTC in feed mixtures. A minimum of 100 fingerling salmon or rainbow trout were used in each experiment.

Species	Diet	Active ingredient (*mg/kg/day*)	Days fed	Acceptability	Per cent body weight fed/day	Per cent antibiotic feed mix in diet
CTC (40 g/pound of feed)						
Sockeye	Dry	250	4	Good	2.0	14.2
Sockeye	Dry	500	4	Good	2.0	27.4
Sockeye	Ore. moist	500	4	Good	2.0	30.0
Sockeye	Dry	700	3	Good	2.0	32.3
Sockeye	Dry	1000	4	Poor	2.0	56.8
Rainbow trout	Dry	1000	4	Good	3.0	28.0
Rainbow trout	Dry	2000	4	Poor	3.0	56.6
Chinook	Ore. moist	500	4	Good	5.0	13.0
Chinook	Ore. moist	500	4	Poor	2.0	28.5
OTC (50 g/pound of feed)						
Sockeye	Dry	250	4	Good	2.0	11.8
Sockeye	Dry	300	4	Poor	2.0	16.0
Sockeye	Dry	500	3	Poor	2.0	22.7
Sockeye	Ore. moist	500	4	Fair	2.0	23.0
Chinook	Ore. moist	250	4	Fair	2.0	11.8
Chinook	Ore. moist	500	4	Poor	2.0	23.0
Rainbow trout	Dry	700	3	Fair	3.0	30.0
Rainbow trout	Dry	1000	4	Poor	3.0	45.5

second day of feeding; only after the third consecutive day of feeding is there definite rejection or acceptance of the diet.

We used water-soluble OTC with glucosamine in our major marking studies; not only was it acceptable at all levels of feeding, but it produced consistently good marks. CTC in feed mixtures, though acceptable at dosages required for marking, was not consistent in marking quality. This inconsistent marking may have been caused by either high levels of calcium in the diet or variations in condition of the fish.

DETECTION OF MARKS

EQUIPMENT

Detection of tetracyclines in bone requires microscopic examination with ultraviolet illumination. The light source used in the laboratory was a 200-w mercury-vapor arc lamp with UG-1 and BG-12 exciter filters. Ultraviolet-excluding objectives and a Wratten 2A eyepiece filter were used to absorb ultraviolet light, but allow passage of visible light through the ocular lenses. Three- and six-power objectives in combination with a 10-power ocular are sufficient for detection of deposited fluorophore.

Examination of samples in the field required portable equipment which included: microscope illuminator with 100-w mercury-arc lamp and transformer; blue pass exciter filter, BG-12 or Corning 5113; ultraviolet pass exciter filter, UG-1 or Corning 5840; and a Wratten 2A microscope eyepiece filter, $\frac{3}{4}$-inch diam, for a standard monocular microscope.

Treatment of Samples

FINGERLINGS

After administration of tetracyclines a general tissue fluorescence persists for several days. Even though deposition in bone is immediate, it is advisable to delay examination at least 1 week to allow for clearance of unbound antibiotic from the tissue and, more important, for additional bone growth. The contrasting bluish autofluorescence of unmarked bone on both sides of the deposited fluorophore allows better definition and evaluation of the quality of the mark. Some initial confusion may result from fluorescence of lipofuscin (yellow) and porphyrins (red). These tissue components, however, do not have the distinctive color characteristics or distribution of tetracycline-induced fluorescence.

Samples which were to be retained for a period of time before observation were frozen. Since normal illumination has a photolytic effect on deposited fluorophore, frozen samples were thawed and cleaned only immediately before observation. Flesh was removed from the bones with boiling water or hot tap water, and the cleaned material kept moist until examination. In most species of fingerling salmon and trout, the marks on the cleithrum or an anterior rib are a reliable index for determining the effectiveness of marking. In chinook salmon fingerlings, however, evaluation of a mark by using an anterior rib is difficult because the flange at the proximal end of the rib is not well developed.

ADULTS

Detection of tetracycline in skeletal tissue requires that the sample be transparent to the exciting ultraviolet wavelengths and the visible light given off by the deposited fluorophore. These requirements are easily met in fingerlings, since most skeletal components are thin and transparent. As growth proceeds, however, changes are induced in the skeletal tissue by overlying bone growth and remodeling which impose limitations on the selection of bones suitable for sampling. Sectioning and grinding of bone samples to expose the tetracycline mark is slow and yields inconsistent results.

Bone samples were taken from coho salmon when they returned as "jacks" (precocious males averaging 1.4 kg) in 1963 and as adults in 1964; they had been marked in 1962 as fingerlings (average weight, 30 g). The gill rakers and vertebral arches of returning jacks were marked, but in adults these structures had been modified by bone reabsorption, and the tetracycline was no longer detectable. The hypurals and cleithrum and the epihyal, ceratohyal, and several other bones of the head become progressively more ossified with increasing size; though the mark in these bones was evident in jacks, the overlaid porous bone obscured the mark in adults. In the vertebral centrum, ribs, and entopterygoid, the deposited tetracycline was easily detected in both jacks and adults.

We also examined adult sockeye, chinook, and chum salmon which were marked with tetracycline as fingerlings, and found the vertebral centrum to be the most reliably consistent bone for detection of deposited fluorophore. Easy detection of marks in the centrum is a result of the growth pattern; no additional bone is laid down over previously existing calcified areas. The branchiostegals and opercular bones, though often well marked in fingerlings, do not retain tetracycline in detectable amounts in adults.

Flesh and cartilage may be removed from the bones of adult salmon with boiling water or hot tap water, but it is more efficient and effective to immerse the bones several hours in a constantly agitated solution of 2% trypsin (1:250 activity). After they are cleaned, bone samples from jack and adult salmon must be kept moist until examination is complete, because dehydration induces opaqueness and radically reduces detection of the deposited fluorophore.

As mentioned earlier, normal illumination and ultraviolet light have a photolytic effect on deposited tetracycline fluorophore. In preliminary studies we found that the scales of fish took up and retained tetracycline. Under laboratory conditions where fish were not exposed to direct sunlight, scale fluorescence persisted at least 13 months; but when fish were retained in outside ponds, scale fluorescence was evident for only 2 or 3 days after completion of feeding. The examination of a scale may be useful, however, for an immediate check on effectiveness of marking.

PERMANENCE OF TETRACYCLINE MARK

A study designed to determine retention and ease of detection of deposited tetracycline was undertaken at the Oregon Fish Commission's Klaskanine Hatchery near Astoria, Oregon. In March 1962 we fed antibiotic to one-sixth of the 1960 year-class of coho salmon at the Klaskanine Hatchery (205,000 fish). OTC with glucosamine mixed in a standard wet diet was fed at a level of 500 mg/kg body weight per day on 2 consecutive days. Cleithra removed from 196 fish 2 days after feeding indicated that 94% of the fish were marked.

The coho salmon marked with OTC were the last fish released from the hatchery. At release they weighed 15 to the pound, identical in weight with unmarked fish released during the preceding 6 weeks. Since 94% of the coho salmon fed OTC were marked, we should expect 17% of all 1960 year-class coho salmon returning to the Klaskanine Hatchery to marks (assuming that the deposited tetracycline was retained, survival of marked and unmarked fish was equal, and straying minimal).

A fraction of the releases returned to the hatchery as jacks after 7 months of oceanic life; 10% of these returnees were sampled for tetracycline marks. In the first 500 fish taken, both the cleithrum and an anterior rib were removed. Intensity and clarity of marks on both structures were comparable; further sampling consisted of anterior rib bones only. In a sample of 1602 jacks, 22% bore a tetracycline mark — or about 5% more than expected.

Beginning in mid-September 1963, 1½ years after release of the marked fingerlings, the commercial fishery at Astoria was sampled. We hypothesized that some of the adults passing through the commercial fishery were of the 1960 year-class — reared at, and returning to, the Klaskanine Hatchery. The Oregon Fish Commission sampled 22% of the coho salmon in the commercial catch by removing the entopterygoid (a paired bone in the roof of the mouth beneath the eye that is not heavily ossified in adults; removal causes no observable mutilation of marketable fish). In 30 marked adult coho salmon the entopterygoid, anterior rib, and vertebral centrum were compared. The entopterygoid was satisfactory in each fish for determining the presence of a tetracycline mark. Of 822 adults from the commercial fishery, 17% were marked. We attributed the lower percentage of marked fish in the fishery samples (compared with the 22% return of jacks in the previous year) to intermingling of unmarked coho salmon from other areas.

By the end of the commercial fishing season, some of the adult coho salmon which had passed through the fishery were already entering the holding troughs at the Klaskanine Hatchery. At the hatchery, we sampled an anterior rib from 10% of the returning adults; of 437 examined, 21.3% were marked—about the same percentage as in returns of jacks in 1962. The percentages of marked adult males and females were not significantly different: 21.6% of 306 females and 20.6% of 131 males were marked.

Among the adult fish sampled at the Klaskanine Hatchery, the 4% increase in marked fish between release and return was probably due to a difference in survival. It is possible that the tetracycline curtailed a disease, or the time of release may have been more favorable for survival. If the tetracycline mark were not retained permanently, or if we were not able to detect the mark adequately, we would have expected a mark recovery of less than 17%.

We also tested the retention of deposited fluorophore after the coho salmon had spawned and died to determine if marked salmon could be identified during surveys on the spawning grounds. Six carcasses of coho salmon which were found to be marked were staked out in a stream in mid-November 1963. In early February 1964, bone tissue from these fish was examined for the tetracycline mark. Fluorescence was observed in the vertebrae in all six fish, and in three fish the anterior rib, though mostly decalcified, showed evidence of deposited fluorophore.

SURVIVAL OF MARKED FISH

SHORT-TERM EFFECT

Tetracyclines are recognized to have a low degree of toxicity for man and other animals, and we observed no distress or mortality after feeding the antibiotics in any of our laboratory or hatchery studies. In one experiment on 25 rainbow trout we fed 5200 mg of pure OTC per kilogram of body weight over 3 consecutive days, and in another study on 1000 chinook salmon fingerlings, we fed 1600 mg of pure OTC per kilogram of body weight per day for 5 consecutive days. In neither experiment was there evidence of toxicity or noticeable changes in behavior.

Studies on humans and other animals (Dessau and Sullivan, 1961; Welch, 1954) have given evidence that high oral doses may cause temporary gastrointestinal irritation. These effects are probably not manifestations of the antibiotic, but expressions of the effects of tetracyclines on the intestinal flora. According to Margolis (1953), fish do not have common bacterial commensals in the intestine, but ". . . the presence of bacterial flora depends solely on the recent intake of food and the degree of contamination of the food and water." This difference may well account for the absence of any adverse behavior in fish that were fed large quantities of tetracycline.

To evaluate short-term mortality after feeding OTC to sockeye salmon fingerlings, fish from the same hatchery lot (i.e. fertilization, hatching time, and handling procedure were similar) were distributed among 12 ponds (6 test and 6 control). In mid-July 1962, the number of fish in each pond was estimated. During 4 days in mid-August, fish in the six test ponds were fed 2 g/kg body weight of OTC with glucosamine in a dry pellet diet. The numbers of fish in each pond were again estimated in mid-October. In addition a record of daily mortality by pond was maintained throughout the study. Two estimates of mortality were derived from these data: one based on the daily mortality count and the other on differences in the estimated numbers in each group before marking with tetracycline and 2 months after marking. The daily mortality counts indicated a slightly, but not significantly, higher mortality for the fish fed tetracycline (Table IV). Even before feeding tetracycline, however, mortality in the test group was higher than in the control group. Mortality based on

TABLE IV. Short-term mortality of sockeye salmon fingerlings fed oxytetracycline (OTC), based on population estimates and on direct counts of dead fish.

Date (1962)	Control		Test	
	Population estimate	Observed mortality	Population estimate	Observed mortality
July 15	381,812		381,301	
August 4–11		429		544
August 12–15[a]		100		112
August 16–23		277		225
August 24–31		191		215
September 1–30		541		602
October 1–16		569		613
October 16	347,644		351,010	
Total mortality	34,168	1,678	30,291	1,785

[a] A total of 2 g of OTC per kg body weight was fed to the test group from August 12 to 15, 1962.

estimates of the number in each pond at two intervals was 9.0% in the control group and 8.0% in the test group. These percentages represent more reliable estimates of mortality than the daily count because the daily count did not include the many unobserved losses that presumably resulted from cannibalism or bird predation.

Long-Term Effect

We initiated a field study in the summer of 1962 to determine if feeding and resulting deposition of tetracycline affected long-term survival. For this study we used sockeye salmon of the 1961 year-class reared at the Leavenworth National Fish Hatchery.

Leavenworth Hatchery is in the State of Washington just east of the Cascade Mountains. Sockeye salmon reared at Leavenworth are released into nearby Lake Wenatchee. After residing there for 7 months, the smolts migrate down the Wenatchee River and into the Columbia River.

Before marking with tetracycline, one-third of the sockeye salmon in each of 30 holding ponds were marked with an adipose-maxillary clip combination. After the fish had attained a count-weight of 125 per pound, we fed OTC with glucosamine and vitamin D (2 g of OTC per kilogram of body weight) in a low-calcium pelletized diet to the fingerlings in 10 of the 30 holding ponds for 4 consecutive days. A sample of 550 fish taken 2 months later from the 10 ponds indicated that 100% of the fish had been marked with the tetracycline.

At release, the entire hatchery production of sockeye salmon was randomly sampled with a 10-pocket sampler. One pocket of the sampler was closed, retaining 10% of the fish. The 10% retained were sampled again. The resulting 1% were then examined to estimate the numbers released in the following categories: 202,000 double marked with OTC and an adipose-maxillary clip; 425,900 OTC-marked only; 369,800 clipped only; and 779,000 unmarked.

In the fall of 1962, the sockeye salmon fingerlings were released in Lake Wenatchee; the following spring they migrated from the lake with naturally spawned sockeye smolts. We collected 2020 sockeye smolts at the lake outlet from April 15 to May 28, 1963. An anterior rib was removed from each fish, and they were checked for clips, measured, and weighed.

Our comparison for determining the effect of OTC on survival is between fish with a double mark (OTC plus clip) and those with clip only. Since both groups were clipped this comparison would show only the effect of tetracycline. Of 748 clipped fish recovered, 34.1% were double marked. At time of release from Leavenworth Hatchery, 35.3% of the clipped fish were double marked. Point estimates and confidence intervals for the percentage of double-marked fish at release and recovery are given in Table V. If administration of tetracycline did influence survival, we would expect the percentage of double marks to be significantly different from 35.3%.

The 1961 year-class of sockeye salmon released from Leavenworth Hatchery was sampled again when the fish returned as adults in the fall of 1965. At that time we removed a vertebra from each of 2050 caught in the commercial

TABLE V. Percentage double marked at release and recovery, and 95% confidence intervals around these percentages, for sockeye salmon marked at Leavenworth Hatchery in 1962, and recovered in 1963 and 1965.

	Sample size	Percentage double marked	95% confidence intervals
Release, 1962	6053	35.3	34.1–36.6
Recovery, 1963	748	34.1	30.6–37.6
Recovery, 1965	166	38.6	30.6–46.6

fishery on the Columbia River, and obtained an additional 4115 vertebrae from spawned-out fish on the Wenatchee River drainage. Among the 6165 fish, 156 fish had an adipose-maxillary clip. Of the clipped fish, 40.4% bore a tetracycline mark, a percentage not significantly different from that observed at time of release (Table V).

This field study showed that the presence of tetracycline in the sockeye salmon's skeletal system did not affect survival during either their 7-month residence in Lake Wenatchee or their 2-year stay at sea.

GROWTH AND LENGTH–WEIGHT RELATION OF MARKED FISH

Several effects of tetracycline on growth are described in the literature. Large or prolonged doses of tetracycline administered during embryo formation tend to retard growth (Rolle and Bevelander, 1966; Saxén, 1965). Postnatal administration of tetracycline, however, often promotes growth (Guerrant, 1963). Bevelander and Goss (1962) demonstrated that regenerating scales of *Fundulus hetercolitus* given daily injections of TC had normal dimensions but contained less calcium. Similarly, Kobayashi et al. (1964) demonstrated that a single dose of tetracycline inhibited mineralization in goldfish scales. We have not noted growth promotion, retardation, or structural weakness in the bone tissue of salmon as a result of tetracycline administration.

As mentioned in the preceding section, seaward-migrating sockeye salmon from Lake Wenatchee were sampled, measured, weighed, and divided into four categories depending on the presence or absence of clips or tetracycline marks. Length–weight relation was calculated for fish of each category upon recovery. The method used in calculation is based on a length–weight relation as described by Rounsefell and Everhart (1953). Within the sample several hundred fish were not included because of incomplete measurements or the presence of 3-year-old sockeye of the 1960 year-class. The values of c and n in the equation $W = cL^n$, where L represents fork length in millimeters for fish 75–125 mm, and W weight in grams, are given in Table VI. The calculations show a decidedly lower constant and exponent for clipped fish as compared with fish that were unmarked or marked only with OTC. The small difference between the tetracycline-marked and unmarked fish demonstrates that administration of tetracycline did not impair growth.

TABLE VI. Length–weight relation ($W = cL^n$) of sockeye salmon recovered at time of migration out of Lake Wenatchee in 1963.

Category	Number of fish	c	n
OTC and clip	144	4.2676×10^{-4}	2.75495
Clip only	269	4.4397×10^{-4}	2.76369
OTC only	242	5.6968×10^{-4}	2.82608
No mark	710	5.9549×10^{-4}	2.83403

In our field study at Klaskanine Hatchery (designed to test permanence of a tetracycline mark) we recorded the fork length of each jack and adult coho salmon sampled upon return to the hatchery. A comparison of length frequencies of jack and adult returnees (Fig. 2) again indicated that tetracycline administration had no effect on growth.

FACTORS IN COST OF MARKING WITH TETRACYCLINE

Several important factors affect the cost of marking with tetracycline. We fed 250–400 mg/kg body weight 3 or 4 consecutive days primarily to obtain 100% marking, and thus reduce one variable in analysis. Evidence from other animals (Dickinson et al., 1955) indicates that once a high level of antibiotic is attained, it can be sustained by lower subsequent doses. Gradual reduction in dosage of tetracycline may result in less than 100% marking, but costs could be cut one-third or more. Also, through use of low-calcium diets and potentiators, costs may be reduced even further by increasing absorption and thus lowering the dosage required to obtain a satisfactory mark.

Another cost consideration is related to the size of the fish at time of marking. Since the amount of tetracycline given is a function of body weight, it appears most economical to mark at the smallest possible size. The amount of fluorophore deposited, however, and hence the intensity of the mark, are partly dependent upon the amount of proliferating bone area available at time of marking. Again, subsequent bone growth and reabsorption are usually greatest in the area of bone origin. Inadequate intensity of the mark and subsequent overlying bone may render detection difficult and increase cost of analysis. To minimize both the cost of marking and the cost of detection, an optimum size for marking should be considered.

SUMMARY

Our studies on Pacific salmon and rainbow trout have shown that oral administration of tetracycline antibiotics in adequate doses causes deposition of fluorescent material on the surface of the growing bone. The resulting mark is readily detectable by fluorescent microscopy and is apparently permanent, since no diminution of the mark occurred in fish recovered 3½ years after marking.

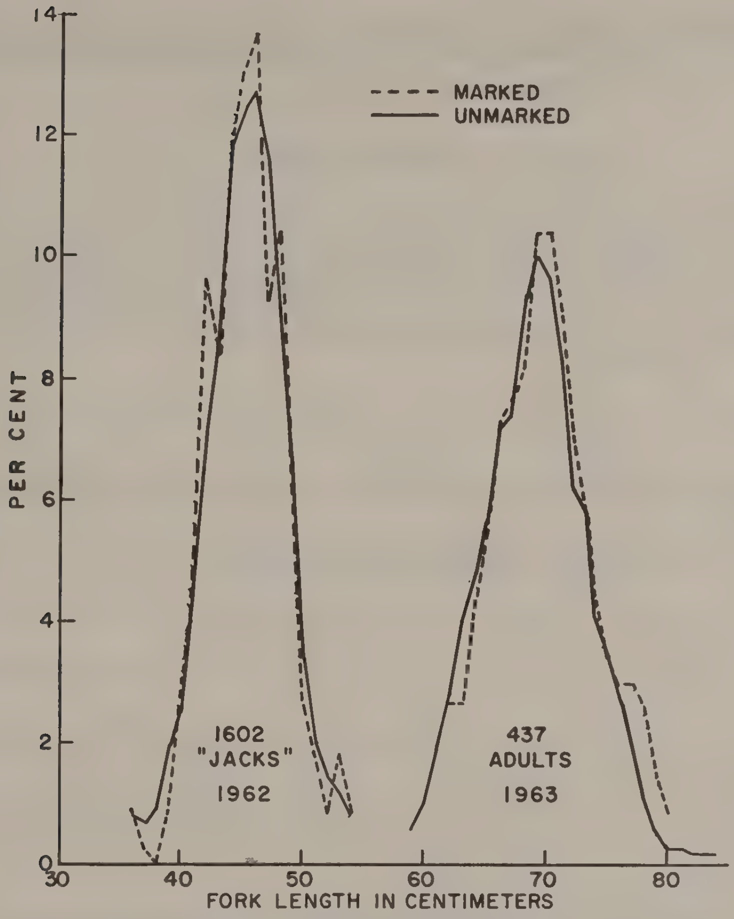

FIG. 2. Length frequencies, in per cent, of tetracycline-marked and unmarked jack and adult coho salmon that returned to Klaskanine Hatchery.

We found that the oral dosage levels necessary for deposition of a detectable mark may be as low as 25 mg per kilogram of body weight per day; but, the most satisfactory and consistent results were obtained by feeding a minimum of 250 mg/kg body weight daily for 3 or 4 consecutive days. There is evidence that absorption of antibiotics from the gut may be increased by using diets with low calcium content and a potentiator; thus the dosage level required for marking may be reduced.

No immediate mortalities from feeding tetracycline antibiotics have been experienced, and all evidence accumulated from field studies indicates no long-term adverse effect on growth or survival.

Marking fish with tetracycline antibiotics offers a number of advantages. Entire hatchery populations may be marked easily without individual handling.

The mark applied is permanent throughout the life of a fish. No mutilation or visible contrast with normal coloration occurs which might cause differential survival among marked and unmarked groups.

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Sedentary Bottom Animals

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An excellent summary of the important role played by sedentary organisms as well as various demonstrations are provided by the author.

Introduction

The objectives of this lecture-demonstration are to: 1) point out the importance of the sedentary organisms in the sea and particularly in the food chain; 2) discuss their foods and feeding habits; and 3) demonstrate the efficiency of filter feeders in removing enormous numbers of phytoplankton from the water.

The sedentary animals, according to strict definition, are those fixed to one spot, as is the barnacle. For discussing the food chains it is necessary to broaden this definition. Therefore three kinds of sedentary animals are recognized: 1) those that are sessile, such as the barnacle; 2) those that burrow but do not move about, such as many of the worms and mollusks; and 3) those that burrow, crawl, or are attached but have a limited movement, such as the anemones, starfish, and some worms and mollusks.

The foods of sedentary animals are grouped into four types: 1) suspended material including plant and animal plankton, and non-living organic particles—all at the mercy of the currents; 2) detritus or bottom deposits including non-living plant and animal debris, and living bacteria and diatoms; 3) larger seaweeds and algal films on rocks and shells; and 4) larger animals.

The sedentary animals also are grouped into four types, directly in relation to their feeding habits: 1) the filter feeders which strain out suspended particles; 2) the detritus feeders which swallow debris with little discrimination and cast out the indigestible material; 3) the grazers and browsers which feed upon algal films or the larger seaweeds; and 4) the predators which prey upon other animals.

The interrelations of foods, feeding habits, and environment are very important to the sedentary animals, since they cannot move sufficiently to change their basic environments if they prove unsuitable. Thus if a young oyster undergoes metamorphosis from the larval stage, settles out of the water, and lands on soft bottom, it may not be able to feed and survive if its gills are clogged by the fine bottom sediments, even though its planktonic food may be abundantly available. Other animals whose anatomies are

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adapted to feeding under such circumstances (many of the worms) could survive. Specialized predators such as the drills, *Polinices* and *Urosalpinx*, are entirely dependent upon the abundance of their mollusk prey. If the mollusks do not set repeatedly and the supply is consumed or otherwise lost, the predator cannot survive. Adaptable predators such as the brittle star, *Amphiura*, are able to feed upon animal food when it is available, and on detritus when no prey is found. These forms may be more important predators than the more active, specialized forms, since they may occur more nearly universally and in greater numbers.

The sedentary animals are important to the food chain for three principal reasons. First, as a group they place a major demand on the available food supplies. They exist in enormous numbers—of an estimated 1,000,000 species of named animals, approximately 10% may be classed as sedentary—and as a group their distribution is universal. The wide variety of foods used places the group in competition with most other animals. Second, the sedentary animals exert an important effect, both physically and chemically, on the bottom and waters in which they live. Their physical influence is exerted principally in changing the character of the bottom. The tube-building worms and crustaceans stabilize shifting sands and make soft, muddy bottoms more firm. The free-moving burrowers repeatedly mix the top layers of sediments. All forms contribute waste or skeletal material to the bottom. The tightly compacted fecal pellets of many of the worms become a characteristic portion of the sediments. The remains of dense beds of mollusks and colonies of corals can produce areas built up appreciably above the surrounding bottom. All forms concentrate various elements and compounds in building their bodies and shells. Either living or dead, these materials provide important sources of elements for other forms of life. The concentration process can be of value to man. Vast deposits of molluscan shells are used in some parts of the world as a source of lime for construction. The ground shells provide calcium for poultry, and in areas where sand and gravel are scarce the shells are used for fill, roads, and sidewalks. Certain tunicates *(Ciona, Ascidia)* concentrate the metal vanadium nearly 300,000 times over its concentration in sea water and have been suggested as a commercial source for this element. The discharge of waste products in general adds to the fertility of the bottom and overlying waters benefiting the primary producers such as bacteria and phytoplankton. Sometimes, notably in dense beds of mollusks, the heavy discharge of feces contains sufficient toxins to reduce growth or kill the nearby animals. Third, the sedentary animals are an important food source for the free-living bottom feeders, the predators. Fig. 1 shows a simplified food chain adapted from Ricketts and Calvin (1952) illustrating the dependence of the sedentary animals on the simpler food forms and in turn the dependence of the predators on the sedentary animals.

Demonstration

By placing common filter feeders in a small aquarium containing a rich suspension of food organisms, a marked reduction in food can be demonstrated during a 1-hour class period.

Into a 20-liter aquarium are placed sea water at room temperature and two dozen or more clams, oysters, or mussels. A few other plankton feeders may be added to increase interest of the members of the

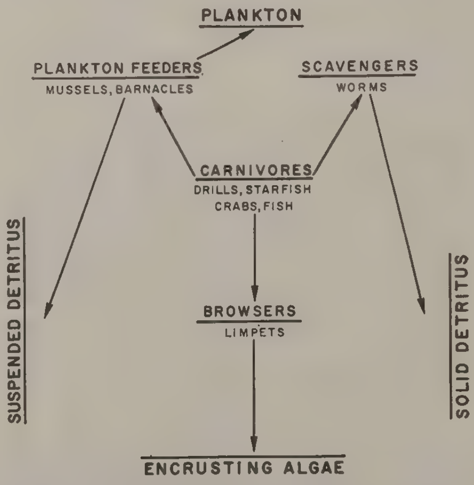

Fig. 1. A simple food chain in a mussel bed. Adapted, with permission, from Ricketts and Calvin (1952).

class. Barnacles, anemones, tunicates, and tube worms have proved suitable. If convenient, the animals may be starved for a day or two by holding them in a limited supply of water. To the aquarium is added a sufficient quantity of a culture of unicellular algae to yield a concentration of 400,000 cells per ml or a total of 8,000,000,000 cells in the 20-liter aquarium. This concentration is not so high as to inhibit feeding, but high enough to stimulate active feeding and to make the water noticeably turbid. The unicellular alga used was *Dicrateria inornata,* but any of several small species could be used. The cultures may be grown in the laboratory (Loosanoff and Davis, 1963) or obtained from one of the several marine laboratories where algal cultures are maintained.

The quantity of cells consumed during the demonstration is determined with the aid of a colorimeter (Bausch and Lomb Spectronic "20"). At the beginning of the class when the aquarium is set up, a sample of the clear sea water is used to zero the instrument. When the algal cells have been added a sample is taken and the optical density is read off the instrument. On a graph with optical density and cell numbers as the two coordinates (Fig. 2) the optical density of the sample is plotted with the known initial number of cells (8,000,000,000). Since optical density varies directly with the number of cells, a line may be drawn from the initial point back to zero.

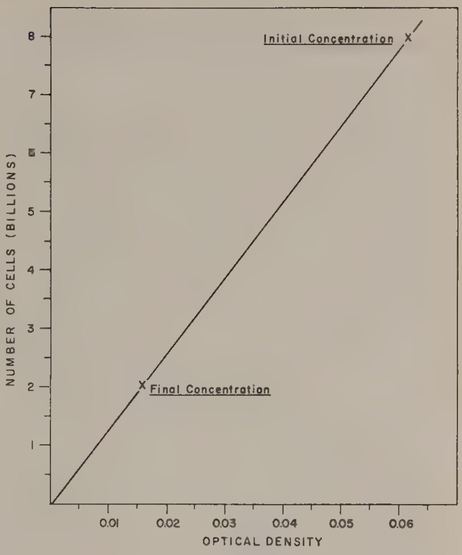

Fig. 2. Typical plot of optical density and cell concentration before and after 45-minute feeding period.

Expected Results

At the end of the class period a final sample is taken from the aquarium, the optical density is read, and the value is plotted on the diagonal line of the graph. The corresponding ordinate is the number of cells left at the time, and the difference between the initial and final numbers of cells is the number consumed during the period. Even if a colorimeter or some device for obtaining a numerical value of turbidity is not available, the difference in concentration may be shown visually. A white card with a sharp, black design or printing, placed at the rear of the aquarium, will be barely visible initially at the prescribed concentration of cells. At the end of the period it should be clearly visible and large printing legible. Readings of percentage transmittance, obtainable from many colorimeters, cannot be plotted in direct (straight line) relationship to cell numbers. A logarithmic scale must be used.

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FEEDING BEHAVIOR OF A YOUNG STARGAZER, *ASTROSCOPUS Y-GRAECUM*.—Certain relatively sedentary marine fishes use specialized appendages as "fishing gear" to attract prey. The Lophiidae and Antennariidae, for example, use modified dorsal spines. The Mediterranean stargazer, *Uranoscopus scaber* (Uranoscopidae), extends a red tongue-like projection from its mouth to attract small fish (Andriashev, 1944). We observed the use of a different type of "fishing gear" in the feeding behavior of an immature stargazer of the genus *Astroscopus*. This behavior included movements of the eye or dorsal fin, or both, as lures.

A young stargazer, *Astroscopus y-graecum* Cuvier, 28 mm SL, was caught in the daytime in a surface plankton tow in Gallants Channel near Beaufort, North Carolina. It was placed in an aquarium containing sea water and a layer of sand about one inch thick and was fed post-larval Atlantic croaker, *Micropogon undulatus* (12–20 mm SL), and post-larval pinfish, *Lagodon rhomboides* (10–15 mm SL). (It is now cataloged as U. S. National Museum 200561.)

When the stargazer was buried in the sand, it used eye movements to attract post-larval fish. The eyes and mouth of our specimen closely resembled the overall appearance of the bottom of the aquarium, and thus were well camouflaged. When a small fish came within 40–50 mm of one side of its head, the stargazer moved the eye on the opposite side in a rapid semicircular motion one to five times, while the eye nearest the prey remained motionless. The moving eye apparently simulated a minute organism burrowing in the sand and decoyed the curious prey to a position directly over the stargazer's mouth. Eye movements were repeated until the prey approached within range or moved away.

A rapid intermittent ripple of the posterior half of the soft dorsal fin also appeared to be used to attract food. The ripple, which was similar to a larger burrowing organism, was used only when potential food approached from the front or the rear. As soon as the prey was attracted within "eye range" of the stargazer, the intermittent fin movement ceased and the eye movements began. When a potential meal came into range, the stargazer lunged upward from its resting position in the sand. These lunges usually occurred when the prey was no more than 10–15 mm away, directly above the mouth, and were so sudden that few fish escaped. Our specimen captured 5–10 post-larvae per day by these movements.

The eyes and fin were used to lure prey only when the stargazer was buried in the sand. When it had not been fed for 24–48 hr, it actively pursued prey that were introduced into the aquarium. After eating several post-larval fish in rapid succession, it returned to its resting place in the sand. During periods when its appetite was apparently appeased, no eye movements were observed and prey swam freely directly over its mouth.

The outward flow of water over the gills and under the curved pectoral fins of the stargazer served as a third mechanism for attracting prey. Small fish were occasionally attracted to the area which Dahlgren (1927) described as "two tiny craters in the sand . . . showing the sand grains dancing up and down continuously as they do in the sand bottom of many springs where the water is welling up."

Our observations revealed that the young of this genus, like the adults, usually feed only in daylight. Our specimen began to feed actively when the lights were turned on in the morning. The number of post-larval fish present in the morning was usually the same as had been present the previous evening. Pickens and McFarland (1964) observed that adult stargazers also do not feed in the dark or when their eyes are covered.

Dahlgren (1927) suggested that adults of this genus are buried in the sand during the day and move about mainly at night. Our immature specimen also remained buried during the day and emerged from the sand only to feed. Much of the movement at night apparently occurred while the fish was buried under the sand. Every morning trails were visible in the sand, and the stargazer was buried at the end of one of the trails.

The adult of this genus shows an association between the eyes, electric organ, and feeding behavior. White (1918) suggested that the electric organ, which was not fully developed in our specimen, is probably operated from the optic centers, since the electroplaxes are derived from certain eye muscles. Pickens and McFarland (1964) demonstrated that an electric discharge occurs when adult stargazers feed, although its function is still unknown. Visual perception of moving prey is needed, however, before the electric discharge occurs. Our observation that immature stargazers use their eyes as decoys demonstrates a further association between the eyes and feeding behavior in this genus.

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INTRODUCTION OF COMMERCIALLY IMPORTANT SPECIES INTO INLAND MINERAL WATERS, A REVIEW

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INTRODUCTION OF COMMERCIALLY IMPORTANT SPECIES INTO INLAND MINERAL WATERS, A REVIEW

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ABSTRACT

The successful introductions of commercially important animals into inland mineral waters of the following four categories were reviewed.

1. *Lagoons.* These have been modified into ponds and used for the culutre of marine animals in Europe and Asia. Milkfish, *Chanos chanos,* cultured most extensively in Asia can survive in ponds with salinities as high as 140 ppt. Mullets, *Mugil* spp., prawns, *Penaeus* spp., and other animals can survive up to 70 ppt in these ponds. In Europe, ells, *Anguilla anguilla,* mullets, *Mugil* spp. and other fishes are cultured in salinities up to 47 ppt.

2. *Relict waters.* To improve the food base for fish, man has introduced additional species of fish and invertebrates into the Caspian Sea (salinity 12 to 13 ppt) and the Aral Sea (10 ppt). The mullets, *Mugil auratus* and *M. saliens,* were introduced and now support an important fishery in the Caspian Sea. *Nereis diversicolor* was introduced as a food for fish in the Caspian Sea. The Baltic herring, *Clupea harengus,* has been introduced into the Aral Sea.

3. *Salterns and inland brines.* Man has successfully introduced fishes into the Salton Sea, California (salinity 33 ppt), and Lake Quarun, Egypt (29 ppt). Nearly the entire fauna of the Salton Sea, in a food chain leading to a sport fish, *Cynoscion xanthulus,* was introduced. Mullets, *Mugil cephalus* and *M. capito,* and the sole, *Solea vulgaris,* were introduced into Lake Quarun and are the objects of a commercial fishery.

4. *Carbonate and sulfate waters.* Whitefish *Coregonus clupeaformis,* were introduced into the Quill Lakes, two saline lakes of Saskatchewan, when the salinities were 11 ppt and 17 ppt. They

supported a commercial fishery for about 10 years until the salinities reached about 19 ppt. Other introductions were made in lakes of various salinities in the region.

The success of the introduction of commercially important species into these waters suggests that further attempts should be made to introduce animals into hypersaline waters. Effluents from desalinization plants could be used for pond culture of fishes and invertebrates. No waters are too saline for the culture of species useful to man; the economically valuable brine shrimp, *Artemia salina*, tolerates saturation.

INTRODUCTION

Man has made few attempts to introduce useful species of animals into hypersaline waters. There are, however, a number of studies that report the successful introduction of commercially important species into inland mineral waters. Characteristically, these inland mineral waters are of varying and increasing salinity. Hedgpeth (1959) gave a classification of inland mineral waters which provides a useful outline. They are:

1. *Hypersaline lagoons with permanent or intermittent connections to the sea.* European and Asiatic pond culture of prawns and fish takes place in man-made or man-regulated lagoons, in which the salinity varies from fresh to near saturation.
2. *Relict waters in which the presence of marine organisms shows a former connection with the sea.* Man has successfully introduced animals into the Caspian Sea (salinity 12 to 13 ppt) and Aral Sea (salinity 10 ppt).
3. *Salterns and inland brines containing principally NaCl.* Almost the entire fauna of the Salton Sea (salinity 33 ppt) was introduced by man, as was the major part of the commercially important fauna of Lake Quarun (salinity 29.4 ppt).
4. *Carbonate and sulfate waters.* Commercial fishes have been introduced into some of the saline lakes of Saskatchewan, whose salinities vary from fresh to near saturation.

SALT WATER LAGOONS AND PONDS

Saline ponds are potentially useful for the increased production of food. Culture of animals, and of plants as their food, in these ponds is a well-developed art that dates back at least 700 years in southeast Asia, and whose origin in Europe is lost in antiquity (Schuster 1952; Frey 1947; Herre 1953b; 1953c; D'Ancona 1954; Chimits 1955; Gopinath 1955; Blanco and Acosta 1958; Kesteven and Job 1958; Vatova 1962).

Ponds have been constructed in the regions of river deltas, in some areas by blocking off a natural bay or lagoon and in others by excavation and use of the excavated soil to embank the pond (Schuster 1952). In these situations the water supply is variable and, as a result, the salinities of ponds vary according to location. The salinity of a particular pond may also vary seasonally by a considerable amount. Djaingsastro (1955) reported salinities in excess of 140 ppt in ponds in Java, and Vatova (1962) reported salinities up to 47 ppt in the "valli salse da pesca" of the Adriatic.

Ponds cover large areas and provide sizable economic returns. In Java (Indonesia) the ponds covered 316,000 acres (128,000 hectares) and produced a crop valued at more than $100,000,000 per year (Ahjar and Tasripin 1955). About 150,000 acres (60,000 hectares) of ponds in the Philippines (Frey 1947) produced 70,000,000 pounds (32,000 kilograms) of fish per year, which were worth $15,000,000 in 1953 (Herre 1953a). Frey (1947) estimated that there were potentially 1,000,000 acres (400,000 hectares) of usable swamps that could be converted to ponds in the Philippines. The "valli" of the Adriatic covered 49,662 acres (20,098 hectares) and the annual value of their production in 1952 was estimated at $1,600,000 (D'Ancona 1954).

Fish culture in salt-water ponds is also practiced in Hawaii, where it apparently is a holdover from aboriginal times (Cobb 1905), and in India, Hong Kong, Singapore, Viet Nam and Thailand (D'Ancona 1954). Salt-water pond culture has been proposed for Australia (Thomson 1955) and other parts of the world (Shelbourne 1964). Tampi (1958) estimated that India had potentially 1.3 million acres (500,000 hectares) of fish farms. In the United States, however, salt-water pond culture of edible animals has been carried out only on an experimental basis, in a few ponds (Johnson 1954; Lunz 1955; 1956; 1958; Shaw 1965). In other than these experimental ponds, fish culture in saline ponds in the United States has not progressed beyond the primitive stage of harvesting species when they enter natural bays and lagoons. This, in spite of the fact that Lunz (1958) presented an economic comparison demonstrating a highly favorable return on an investment in pond construction and culture of shrimp compared to the return on the same investment in a shrimp trawler. A $40,000 shrimp trawler might yield a high of 50,000 pounds (23,000 kilograms) of shrimp per year, whereas, the same capital would purchase 80 acres (32 hectares) of shrimp ponds with much lower operating costs than would be required by the vessel and might yield 40,000 to 80,000 pounds (18,000 to 36,000 kilograms) per year (estimate based on yields in India).

Shaw (1965) stated that commercial pond culture of oysters in the U.S. is 100 years behind that of Europe. Salt-water pond culture of fishes and shrimp in the U.S. is at least 700 years behind that of Asia. As we all know, the trend in the U.S. is to dredge or fill estuarine lands, or to divert the inflow water. These changes lead to reduced production of shrimp and fish. Saloman (1965) showed that dredge-and-fill operations have reduced bait shrimp habitat in Tampa Bay, Florida, by 80 to 90% since 1920; in 1954 to 1962, the catch declined from 4.5 to 0.3 million shrimp. Many similar examples could be cited.

Chapman (1960) proposed that the utility of such areas is to be realized by damming off and draining them so they can be put into agricultural production. As a counter proposal, I suggest that they be dammed, flooded to a depth of 3 or 4 feet and stocked with appropriate species of fish or shrimp.

Culture of milkfish, Chanos chanos. Culture of *Chanos* is on a larger scale than that of any other salt-water species. It is the principal species of culture in the salt-water ponds of Java (Schuster 1952) and of the Philippines (Frey 1947; Herre 1953a; 1953b). Important pond culture for *Chanos* is also carried out in the Celebes, Sumbawa, Formosa, North Sumatra and Hawaii.

Chanos is a marine fish that occurs in the Pacific Ocean from the Red Sea and east coast of Africa to the coast of Central America and the Gulf of California, and from southern Japan to New Zealand. Herre (1953b, p. 457) stated "This means that some day our descendants may see bañgos (milkfish) cultivated over much of this vast area, with great benefit to the people inhabiting a large part of the Indo-Pacific island world, as well as the lowlands of the south and southeast of Asia."

Djaingsastro (1955) observed the lethal salinities for certain species and found the lethal salinity for *Chanos* to be 140 ppt, when the salinity was gradually increased.

Curiously, the milkfish is not important in the commercial catch in the sea, but achieves its importance almost entirely through pond culture (Schuster 1952; Herre 1953a; 1953b). *Chanos*, an herbivorous fish, feeds low on the food chain, and achieves large production. Details on the culture methods practiced can be found in Schuster (1952) or Herre (1953b; 1953c). Since the fish does not spawn in captivity, fry are collected in the sea and transported to the ponds. Because milkfish must be obtained from the open sea, pond culture depends on introduction of larvae and fry. The capture of young and their transportation, sometimes over great distances, is the basis of an industry in itself.

Culture of tilapia, Tilapia mossambica Peters. Recently introduced into pond culture is *Tilapia mossambica* Peters. Chimits (1955) provided an excellent review of the culture of tilapia and its history.

At one time it was thought that tilapia would replace the milkfish as the principal fish in brackish-water pond culture. The market price is lower for tilapia, however, than for the milkfish and prawns. In addition, tilapia is subject to stunting if not cropped heavily or if the waters are not heavily fertilized. Thus, the harvest may consist of fish not of prime marketable size; tilapia is now regarded as a pest in some parts of the Philippines (Rabanal and Hosillos 1958).

Tilapia culture has recently declined somewhat after an initial rapid development (Chimits 1957). The discovery that all-male offspring results from a cross of subspecies of *T. mossambica* may make possible the control of the stocking rate without reproduction in ponds and lead to a revival of interest in tilapia culture (Hickling 1963).

Tilapia mossambica tolerates salinities in the range of fresh to 40 ppt, but does not reproduce above 30 ppt (Chimits 1955). Stunting, as a consequence of overpopulation, can, therefore, be prevented by keeping salinities in ponds greater than 30 ppt. The species was first introduced from Africa into Java in 1939. During the war, the Japanese introduced it into most of the islands of Java (Indonesia), Malaya and Formosa for food production.

Chimits (1955; 1957) listed 38 countries where tilapia is used in fish culture and 10 countries in which it has become established in the wild. More recently, the species has become established in the United States. St. Amant (1965) reported it in California and Springer and Finucane (1963) reported a related species, T. *heudeloti,* in Florida.

Culture of mullet, Mugil spp. In most of the countries where the milkfish are cultured, mullets are also raised (Herre 1953c; Blanco and Acosta 1958; Schuster

1952). Most operators attempt to maintain pure cultures of milkfish, but in some ponds juvenile mullet are accidentally carried into the pond during filling.

Five species of mullet (Table 1) are cultured in the salt-water ponds of the Adriatic in salinities as high as 47 ppt (D'Ancona 1954; Vatova 1962). In this region, the mullet fry are sought in the ocean and stocked in the ponds. Mullet are also raised in brackish-water ponds in other parts of the world; *e.g.*, India (Tampi 1958), Hong Kong (Herre 1953c) and Japan (Blanco and Acosta 1958). They are harvested from ponds in 6 to 8 months, as are the milkfish.

The upper limit of salinity tolerated by *Mugil* is not known but is probably near 100 ppt (Breuer 1957). The highest salinity recorded by Simmons (1957) in waters of the Texas Laguna Madre, where *M. cephalus* are found, was 80 ppt. Zenkevich (1963) reported *M. cephalus* in the Sivash, a lagoon in the Sea of Azov, in a salinity of 60 ppt. Djaingsastro (1955) found that a mullet, *Mugil* sp., did not survive at salinities above 70 ppt in the salt-water ponds of Java.

Miscellaneous species cultured in salt-water ponds. Some 15 species of shrimps and prawns are reared in salt-water ponds in Asia and the far east (Kesteven and Job 1958). In India, prawn culture is carried out in alternation with cultivation of rice in over 10,000 acres (4,000 hectares) which produce about 9,600,000 pounds (4,400,000 kilograms) of prawns per year (Gopinath 1955). Salinities are normally less than 32 ppt. Djaingsastro (1955) reported that lethal salinity for prawns in Indonesian ponds was near 70 ppt. Complete instructions for the culture of a shrimp, *Penaeus japonicus*, including its spawning and rearing of larvae in aquaria until they are large enough for ponds, can be found in Fujinaga (1963). This species reaches commercial size in 1 year.

The puffer, *Fugu rubripes* (Temminck et Schlegel), is cultured in seawater ponds in Japan (Takai *et al.* 1959). Salinities of the ponds are variable and some have little or no tidal exchange. Fifteen other species of fish occur in these ponds. *Mugil cephalus* is very common.

In addition to the five species of mullet mentioned above, the salt-water ponds of the Adriatic are used for eels, *Anguilla anguilla* L., gilthead, *Sparus auratus* (L.), and sea bass, *Morone labrax* Cuv. (Table 1). All are introduced as elvers or fry. A number of other species occur incidentally, the most important of which is a flounder, *Pleuronectes flesus* (D'Ancona 1954).

TABLE 1

Species of fish reared in salinities to 47 ppt in the valli salse da Pesca[1]

Common name	Scientific name
Eels	*Anguilla anguilla* L.
Gilthead	*Chrysophrys aurata* L.
Bass	*Labrax lupus* Cuv.
Mullet	*Mugil auratus* Rissp
Mullet	*M. capito* Cuv.
Mullet	*M. cephalus* Cuv.
Mullet	*M. chelo* Cuv.
Mullet	*M. saliens* Risso

[1] From Vatova (1962).

Culture of oysters in salt-water ponds has been carried out extensively in Europe (Dean 1892; 1893). Recently, his idea that oyster culture should be tried in the U. S. has been revived (Lunz 1956; Loosanoff 1956; Carriker 1959; Shaw 1965). In spite of some promising experimental work, commercial application of the knowledge has not been attempted.

Harvest of brine shrimp, Artemia salina. When salinities become excessive for fish, or in isolated or temporary salt ponds in which there are no predatory fish, the brine shrimp is almost certain to be found. It spreads by way of its amazingly resistant eggs or cysts, which are carried by the wind, by birds and other animals; or they may simply remain dormant on the dry earth for years. The eggs can survive a temperature of −190 C for 24 hours and extreme lack of moisture and oxygen as shown by their survival for 6 months at high vacuum, 10^{-6} mm Hg (Whitaker 1940). The adults live in salinities up to saturation and can reproduce at that concentration (*see* Littlepage and McGinley 1965).

An important industry for brine shrimp exists in the United States, primarily to supply food for aquarium fishes (Dempster 1953) and, more importantly perhaps, food for aquatic laboratory animals of all sorts. At present three commercial operators are licensed to harvest brine shrimp eggs from the shores of Great Salt Lake (D. C. Hales, personal communication). In 1964, they harvested 173,000 pounds (78,000 kilograms) of brine shrimp eggs (Donald Andriano, Utah Department of Fish and Game).

Brine shrimp eggs are not difficult or expensive to harvest because they float to the surface and are washed ashore in windrows. Hales and Bangerter (1957) reported finding 1,000 pounds (450 kilograms) of eggs on the shore of Great Salt Lake in an area 10 by 50 feet (3 by 15 m). They estimated a cost of 8¢ per pound for collecting the eggs.

Adults and eggs are also harvested incidental to salt production in evaporation ponds in San Francisco Bay and San Diego Bay. Highest prices are obtained for the eggs which are vacuum packed and sold by the gallon. There are about 4 pounds per gallon (0.5 kilograms per liter) and they are valued between $3.00 per pound for Great Salt Lake eggs and $8.00 per pound for San Francisco Bay eggs which supposedly yield larger, more nutritive nauplii.

I estimate that the three Great Salt Lake operators grossed over half a million dollars in this business in 1 year. Schmitt (1965) estimated the value of the brine shrimp operation at $350,000 in San Francisco Bay, $25,000 in San Diego Bay and $30,000 in Mono Lake, California. The value of the harvest of brine shrimp adults and eggs from two saline lakes in Saskatchewan, Canada, varied between $150,000 and $450,000 a year from 1963 to 1965 (value estimated from harvest figures supplied by G. E. Couldwell, Department of Natural Resources, Saskatchewan, personal communication).

RELICT WATERS: CASPIAN SEA AND ARAL SEA

CASPIAN SEA

The Caspian Sea is partly of fresh-water and partly of marine origin, as reflected in its fauna. Being 92 feet (28 m) below sea level, it has no outlet and its salinity is destined to increase gradually as a result of evaporation. Evaporation carries off a volume of water equal to the inflow. The net effect of the inflow is to add the minerals it carries to the minerals in the Caspian Sea and thereby increase the salinity. It is the world's largest landlocked body of water; the area is 275,000 square miles (712,000 square kilometers). Its salinity is 12 to 13 ppt. Evaporation from the surface is 2.8 feet (86.6 cm) per year. Shallow bays on its eastern shore have salinities that exceed 200 ppt. The high rates of evaporation from some of these areas, which must be balanced by inflow from the Caspian Sea, may be a mechanism which retards the increase in salinity of the Caspian Sea proper (Twenhofel 1932, as quoted in Emery and Stevenson 1957).

The 78 species of fish in the Caspian Sea accounted for 65.4% of the 1954 Russian fisheries yield. (This percentage must be much less today because of the recent increase in Russian fishing in the world's oceans.) The 78 species represent 17 families; of fresh-water, Mediterranean and Arctic origins.

Between 1900 and 1951 the introduction of 14 species was attempted, but only 8 were established. Four Mediterranean species of fish, of three families, and four invertebrates, as food for fish (Table 2), were deliberately introduced (Zenkevich 1957; 1963).

History of introductions. In the late 1800's and early 1900's attempts to introduce an oyster and the mussel, *Mytilus*, failed. In 1930 and 1931, a flounder, *Pleuronectes flesus*, was introduced. It has never been abundant, though occasional specimens are still caught. One other flounder, *Rhombus maximus*, was planted but did not succeed.

In the early 1930's two species of mullet, *Mugil auratus* and *M. saliens*, from the Sea of Azov were successfully introduced. They are found primarily in the southern part of the Caspian Sea where they support a substantial commercial fishery.

Two shrimp species, *Leander squilla* and *L. rectirostris*, were stocked in the 1920's and now thrive in the Caspian Sea. A mullid, *Mullis barbatus*, and an engraulid, *Engraulis encrasiocholus*, from the Sea of Azov failed to become established.

TABLE 2

Useful animals introduced into Caspian Sea [Salinity 12 to 13 ppt[1]]

Common name	Scientific name	Year
Fishes		
Mullet	*Mugil auratus*[2]	1930's
Mullet	*Mugil saliens*[2]	1930's
Flounder	*Pleuronectes flesus*[3]	1930, 1931
Mosquitofish	*Gambusia affinis*	1920's
Invertebrates		
Shrimp	*Leander squilla*	1920's
Shrimp	*Leander rectirostris*	1920's
Worm	*Nereis diversicolor*	1939, 1940
Mollusk	*Syndesmya ovata*	1939, 1940

[1] From Zenkevich (1957; 1963).
[2] Important in the commercial fishery.
[3] Minor part of the commercial fishery.

Introduction of *Nereis diversicolor* was a well conceived move to improve the food base for fishes. It was notably successful in providing an additional, and more nutritious, source of food for sturgeons. In the period 1939 to 1941, about 65,000 *Nereis* were planted in the Caspian Sea. By 1944, they were a principal food organism for sturgeons in the northern part of the Caspian Sea. By 1948, the worm was present in an area of 12,000 square miles (30,000 square kilometers). Their weight was as much as 86 gm per m^2 of bottom. *Nereis* is an especially valuable adjunct to the fauna because of its behavior. The worm lives in soft silt at the bottom and can survive short periods without oxygen. After it lives for 1 year in the silt it becomes free swimming, spawns and dies, at which time it is readily available as fish food. In this way, it recycles material otherwise lost in the bottom.

Accidental introductions. The construction of the Volga-Don Canal in 1952 led to the accidental introduction of numerous species, many of them harmful fouling organisms carried by ships. The canal provided a route for migration between the Baltic Sea and the Caspian Sea. Zenkevich (1963) held that it will probably lead to the reconstruction of the Caspian fauna. He listed 11 invertebrates (including 2 barnacles and the harmful crab, *Rhithropanopeus harrisii*) and 10 species of algae that have entered the Caspian through the canal. In the same way, five Caspian species have emigrated to the Baltic Sea. One of them, *Cordylophora caspia,* is becoming cosmopolitan and has already been reported occurring in large seaports in North and South America, Australia, New Zealand and China.

Another bivalve mollusk, *Mytilaster* sp., was introduced into the Caspian Sea accidentally, probably carried on the hulls of small vessels from the Black Sea in 1917 to 1920, and by the 1940's was the most abundant benthic species (90% of the benthos). An accidentally introduced diatom, *Rhizosolenia calcar-avis,* is the dominant species in the phytoplankton.

ARAL SEA

The Aral Sea has an area of about 24,900 square miles (64,490 square kilometers), a maximum depth of 223 feet (68 m) and a salinity of 10 ppt (Zenkevich 1957). The ionic composition of the water clearly indicates a freshwater origin, and its fish fauna is entirely freshwater. There are, however, a few marine elements in the flora and fauna.

The introduction of Baltic herring, *Clupea harengus membras* L., into the Aral Sea (Bikov 1960) is another example of the introduction of species into a relict sea. Prior to the introduction of Baltic herring no Clupeids were present in the lake.

Zenkevich (1963) mentioned, besides the Baltic herring, the attempted introduction of five additional species of fish; two bullheads (gobies), *Pomatoschistus caucasicus* and *Gobius melanostomus,* a sturgeon, *Acipenser stellatus,* and mullets, *Mugil auratus* and *M. saliens.* It is not clear that any of these fish have been successful. A fish, *Atherina mochon,* was accidentally introduced. In 1958, attempts were made to introduce two species of *Leander,* from 1954 to 1956, attempts were made to establish three mysids, *Mesomysis kowalewski, Mesomysis intermedia,* and *Paramysis baeii.*

SALTERNS AND INLAND BRINES: SALTON SEA AND LAKE QUARUN

SALTON SEA

The Salton Sea has an area of about 340 square miles (880 square kilometers) and a maximum depth of about 40 feet (12.2 m). Like the Caspian Sea, the Salton Sea is below sea level (235 feet or 71.6 m). Salinity in 1964 was 33 ppt. It is located in a region with a severe desert climate. Failure of an irrigation headworks on the Colorado River in 1905 led to the accidental diversion of the entire river flow into the Salton Sink, creating the modern Salton Sea (Carpelan 1961). Not until 1907 was the river diverted back into its original channel. By that time a fresh-water lake covering 410 square miles (1,100 square kilometers) had been formed. In the late 1930's, construction of Hoover Dam allowed extensive irrigation of the region around the Salton Sea and the sea has since been used as a drainage basin for waters from irrigated lands. Sufficient water must be applied to these fields to carry salts down through the soils and counteract the effects of evaporation.

Initial rapid increase in the salinity was caused by solution of minerals from the bed of the lake (Hely *et al.* 1966), but the later increase in salinity of the Salton Sea is traceable to the inflow of irrigation water (salinity about 2 ppt) balanced by evaporation rates of about 6 feet (1.8 m) per year. The minerals in this irrigation water are of course left behind and cause an increase in the salinity of the lake. Estimates of future salinity depend on assumed values for inflow, but Hely *et al.* (1966) state that by 1980 it could be as low as 31 ppt or as high as 120 ppt.

Faunal history. In 1916, a freshwater fauna, consisting of (in order of abundance) carp, *Cyprinus carpio*, striped mullet, *Mugil cephalus*, humpback sucker, *Xyrauchen texanus*, bonytail, *Gila robusta*, rainbow trout, *Salmo gairdneri* ("fairly common"), and the desert pupfish, *Cyprinodon macularius*, was present in springs around the periphery (Evermann 1916). According to Hely *et al.* (1966) the salinity in 1916 was 16 ppt.

By 1929, the salinity had increased to 33 ppt and the carp and bonytail had disappeared, the mullet had become scarce, but trout were still present near the inlets (Coleman 1929).

As recently as 1952, the Salton Sea contained only four species of fish. Three were small species not useful to man and limited, for the most part, to shallow waters near shore. The fourth species, the mullet, *Mugil cephalus*, is not particularly prized as a food fish in the United States and is not normally considered a sport or game fish, although a small commercial fishery for it existed in the Salton Sea at one time (Hendricks 1961). The mullet has never spawned in the Salton Sea and depends on natural recruitment from the Gulf of California. Juvenile mullet enter the Colorado River from the Gulf of California and pass through irrigation laterals to the Salton Sea.

History of introductions. After a survey in the late 1920's (Coleman 1929), biologists of the California Department of Fish and Game began attempts to introduce desirable species of fish into the Salton Sea. Because of the very limited fauna in the Salton Sea, it was essential to introduce invertebrates as food for fish (Table 3). The successful introduction of *Neanthes succinea* in 1930 was the key to the success of the whole enterprise.

Attempts have been made to introduce a total of 29 invertebrates. Most were chosen for their potential value in enlarging the food base for fish. Only 2 of the 29 species have successfully become established (Carpelan 1961); the pile worm, *Neanthes succinea*, and the amphipod, *Carinogammarus mucronatus*. The amphipod was introduced incidentally during attempts in 1957 to introduce, from Texas, the shoal grass, *Diplanthera wrightii*, as a food for water fowl. The plant was not successful, but the amphipod associate of the grass was established and is utilized as food by fish. A barnacle, *Balanus amphitrite* Darwin, was probably brought in by seaplanes in the 1940's.

Introductions of 35 species of fish were attempted during the period 1929–56. In all, four of these species have become established in the Salton Sea (Douglas 1953; Walker *et al.* 1961).

The mudsucker, *Gillichthys mirabilis*, was the first successfully introduced fish in 1930.

The bairdiella, *Bairdiella icistius*, was introduced in very small numbers (67 individuals) during 1950 and 1951. Its spawning in 1952 marked the first occupation of Salton Sea by a fauna destined to support a sport fishery. Although bairdiella is not a desirable sport fish, because of its small size (11 inches maximum total length), it did fulfill an essential role in the food chain. Bairdiella

TABLE 3

Present fish and invertebrate fauna of the Salton Sea and its origin [Salinity 33 ppt[1]]

Common name	Scientific name	Introduced by man	Date	Self-introduced through irrigation canals	Native fauna
Fishes					
Orangemouth corvina	*Cynoscion xanthulus*	X	1950–56	.	.
Sargo	*Anisotremus davidsoni*	X	1951	.	.
Bairdiella	*Bairdiella icistius*	X	1950–51	.	.
Mudsucker	*Gillichthys mirabilis*	X	1930	.	.
Striped mullet	*Mugil cephalus*	.	......	X	.
Threadfin shad	*Dorosoma petenense*	.	......	X[2]	.
Mosquitofish	*Gambusia affinis*	.	......	.	X[3]
Desert pupfish	*Cyprinodon macularius*	.	......	.	X
Invertebrates					
Pile worm	*Neanthes succinea*	X	1930	.	.
Amphipod	*Carinogammarus mucronatum*	X	1957	.	.
Barnacle	*Balanus amphitrite*	X	1944?	.	.
Copepod	*Cyclops dimorphus*	.	......	.	X
Nematode	*Spilophorella* sp.	.	......	.	X
Rotifer	*Brachionus plicatilis*	.	......	.	X
Protozoa	Numerous species	.	......	.	X

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[1] From Carpelan and Linsley (1961) and Walker, Whitney and Barlow (1961).
[2] Introduced by man into Colorado River (Kimsey 1954), from whence it spread to the Salton Sea.
[3] Introduced by man into area prior to formation of Salton Sea.

feed on *Neanthes* in the deeper waters of the Salton Sea, and thus form a link between *Neanthes* and larger predators.

The success of the larger predator, the orangemouth corvina, *Cynoscion xanthulus*, was dependent on the success of the bairdiella and the two will be discussed together. The corvina spawned in 1952, but less successfully than the bairdiella (Walker *et al.* 1961). The corvina was derived from the introduction of about 200 fish in 1950 and 1951. Although the success of bairdiella in the Salton Sea was sudden and represented a "population explosion," the corvina population developed slowly (Whitney 1961) because the juvenile corvina had to compete for food with the bairdiella. Young-of-the-year of both species fed on copepods, barnacle nauplii and, later, *Neanthes* (Quast 1961; Whitney 1961). The 1953 year class of overpopulated bairdiella was stunted, and succeeding year classes were suppressed because of competition with this year class. Each intervening year class until 1957 was somewhat more successful than the preceding one as mortality gradually reduced the numbers of the 1953 fish. The success of the corvina year classes followed the same course. Once the corvina of a particular year class reached a size where they could begin to feed on bairdiella, their growth rate increased suddenly. Numbers of young-of-the-year bairdiella were sufficient by 1955, that the corvina could shift from feeding on *Neanthes* to feeding on fish at an early age. Large numbers of corvina of this year class were found, and succeeding year classes were even more abundant. The corvina was well established in Salton Sea after 1955 and introductions were terminated in 1956.

Another species which was slow to become abundant was the sargo, *Anisotremus davidsoni*. Fifty-seven individuals were stocked in 1951 by the California Department of Fish and Game. They were rare in 1954–57, when only three specimens were caught in samples of more than 30,000 fish, but by 1960 the species was sufficiently abundant to support a sport fishery.

The threadfin shad, *Dorosoma petenense*, was accidentally introduced into the Salton Sea. By September 1955 it had spread into the Salton Sea through irrigation laterals, after having been introduced in the Colorado River in November 1954 (Kimsey 1954). It does not spawn successfully in the lake, but is recruited from the freshwater inlets (Hendricks 1961).

The corvina, sargo, and bairdiella now support a sport fishery worth $3,000,000 per year (Pomeroy *et al.* 1965). Estimated catch in 1965 was 540,000 corvina, 145,000 sargo and 148,000 bairdiella (unpublished estimates, courtesy R. Hulquist and J. St. Amant, California Department of Fish and Game). The catch and effort are on the increase.

Future of the Salton Sea fishery. The present fish fauna consists of eight species, including the four species present before 1952 (only one of which, *Gillichthys*, had been intentionally introduced by man) and the four recently introduced species (the corvina, bairdiella, sargo and threadfin shad).

The very simple combination of species in the Salton Sea uses the available energy in a food chain leading to the corvina. Walker *et al.* (1961) recommended that no further introductions of fishes be attempted because of the demonstrated success of the present combination of species and because of the danger of introducing undesirable species. On the other hand, the invertebrate food chain seems weak because *Neanthes* is the single food source consisting of individuals large enough to support the fish serving as the principal prey for corvina. The introduction of mysids and amphipods was recommended.

The gradually increasing salinity of the Salton Sea, unless checked, will someday eliminate the fish population. Walker *et al.* (1961) estimated that the sport fishery might terminate after the decade 1980–90. They assumed a maximum salinity tolerance of about 45 ppt and that the salinity would continue to increase at 0.4 ppt per year. Studies of salinity tolerances for related fishes in the Texas Laguna Madre (Simmons 1957) suggest that they might have underestimated the salinity tolerance of these fishes by 10 or even 20 ppt, although the more important species in the Salton Sea have not been studied. Sport fishery and other recreational uses of the Salton Sea have stimulated recent studies of the factors affecting the salinity of the Salton Sea and led to suggestions for controlling the salinity by removal of water either by pumping or by constructing a system of dikes to limit the surface area and reduce the quantity of water evaporated (Hely *et al.* 1966). Eventually it will be necessary to regulate the salinity of the Salton Sea, if the sport fishery is to be maintained. The time is approaching when this step can be economically justified.

LAKE QUARUN

Introduction of fish species into an inland saline lake in a climate similar to that in the region of the Salton Sea was reported by El Zarka (1963). Lake Quarun in Egypt is a small lake of 53,000 acres (22,000 hectares) and has a maximum depth of 26 feet (8 m). Average noon air temperatures range from 17.6 C in January to 34.2 C in July. Evaporation from the surface of the lake amounts to about 6 feet (1.8 m) per year. The use of the lake as a storage basin for overflow from the Nile, the water from which was retained for use during the dry season, originated in prehistoric times and continued until 1920. Subsequent to the construction, in the 1920's, of the Fayoum irrigation system upstream from Lake Quarun, the lake has served as a drainage basin for irrigated lands. Its salinity increased from 11.6 ppt in 1920 to 29.4 ppt in the 1960's. The original freshwater fish fauna of six principal species was eliminated by 1936, except for the presently dominant *Tilapia zilli.*

In 1928–35, mullet, *Mugil cephalus* and *M. capito,* were successfully introduced (Table 4) from the Mediterranean (Faouzi 1936). They have supported a sizable commercial fishery. By 1935, the commercial catch amounted to 377 tons

TABLE 4

Fishes introduced into Lake Quarun, Egypt [salinity 29.4 ppt[1]]

Common name	Scientific name	Year
Striped mullet	*Mugil cephalus*	1928–35
Mullet	*Mugil capito*	1928–35
Sole	*Solea vulgaris*	1938–48

[1] From El Zarka (1963).

(341,726 kilograms) per year. They are still an important part of the commercial catch—18% of the total lake catch.

Fishing has been further augmented by the introduction of a Mediterranean sole, *Solea vulgaris.* A total of 1,603 individuals were stocked over a period of 10 years and commercial fishing for the species began in 1943. In 1960, the most recent year reported by El Zarka (1963), the catch was 151 tons (136,849 kilograms). The largest catch of 299 tons (271,035 kilograms) was recorded in 1959. The catch of sole represents 37% of all species from the lake, and exceeds the catch of that species from the Mediterranean.

CARBONATE AND SULFATE WATERS: SALINE LAKES OF SASKATCHEWAN

This section should perhaps be a subsection under the previous category since the two are obviously related. Clarke (1911) reviewed the history of these waters, explaining it as being the result of differential solubility of naturally occurring ions. Carbonate and sulfate waters became sodium and chloride waters. Moore (1952) reported the precipitation of carbonates and sulfates with increasing concentration of ions in the saline lakes of Saskatchewan.

These Saskatchewan lakes are glacial remnants without outlets. The salinity varies from lake to lake, from less than 0.3 to 120 ppt (Table 5), and increases annually at a rate depending on the size of the lake and its inflow.

None of these lakes is of the chloride type. The dominant ions are bicarbonate and sulfate. They are similar in many respects to lakes of the Siberian steppes and to Devils Lake, North Dakota.

The potential of the saline lakes of Saskatchewan as producers of commercial fish was apparently first recognized by Huntsman (1922) and later documented by Rawson and Moore (1944). Huntsman's experiments in the introduction of cisco, *Coregonus artedii,* and whitefish, *C. clupeaformis,* into the Quill Lakes in the years 1924–27 were successful. Both species survived and supported a commercial fishery. In 1920, the salinity was 10.8 ppt in Little Quill Lake and 16.5 ppt in Big Quill Lake; but by 1944, the salinities had reached 20 ppt and 29 ppt, respectively, and the fish were no longer present (Rawson and Moore 1944). In

TABLE 5

Number of asline lakes in Saskatchewan with the list range of salinities[1]

	Number of lakes	Salinity (ppt)
	1	120
	7	10–30
	19	1–10
	22	0.3–1
	11	< 0.3
Total	60	...

[1] From Rawson and Moore (1944).

the intervening years, up to the early 1940's, five species of fish were successfully introduced into saline lakes (Table 6).

One of the lakes, 27-square-mile (70 square kilometers) Redberry Lake, had a salinity of 15 ppt in 1944 (Rawson 1946). The existing fish population consisted of fathead minnows, *Pimephales promelas,* and two species of stickleback, *Eucalia inconstans* and *Pungitius pungitius.* In the period 1940–44, the lake was stocked with 500,000 to 1,000,000 whitefish, *Coregonus clupeaformis,* fry per year. The introduction was successful and by 1946 the commercial catch of whitefish from Redberry Lake amounted to 20 tons (18,000 kilograms) per year. Rawson found that the rate of growth of whitefish was twice that in neighboring lakes, but he found no evidence of natural spawning. The whitefish were of exceptional quality, particularly because of the absence of parasites in their flesh, a feature which lowers their quality in many other waters.

THE FUTURE

Animals which have been most successfully introduced or cultured in saline waters, and therefore, can be considered to have a high probability of success in future attempts, are as follows:

Fishes
- Family
  - Mugilidae—*Mugil cephalus* introduced into Lake Quarun, self introduced in Salton Sea, and cultured in saline ponds in Europe and Asia. *M. capito* introduced into Lake Quarun and Caspian Sea and cultured in saline ponds in Europe. *M. auratus* also introduced into Caspian Sea and cultured in saline ponds in Europe. Other species of *Mugil* cultured in saline ponds in Europe and Asia.
  - Elopidae— *Elops hawaiiensis* and *Megalops cyprinoides* cultured in saline ponds in Asia. *Elops affinis* self introduced for a short time in Salton Sea. (Dill and Woodhull 1942)
  - Pleuronectidae—*Pleuronectes flesus* introduced into Caspian Sea and cultured in saline ponds in Europe.
  - Soleidae—*Solea vulgaris* introduced into Lake Quarun.
  - Clupeidae—*Clupea harengus* introduced into Aral Sea. *Dorosoma petenense* introduced into Salton Sea.

Table 6

Introduction of fish into saline lakes of Saskatchewan[1]

Common name	Lakes attempted	Lakes successful[2]
Walleye	15	12
Yellow perch	12	7
Lake whitefish	6	4
Northern pike	6	2
Cisco	3	2
Largemouth bass	13	0

[1] From Rawson and Moore (1944).
[2] Successful was defined as surviving in considerable numbers for at least 5 years.

Sciaenidae—*Cynoscion xanthulus* and *Bairdiella icistius* introduced into Salton Sea.

Chanidae—*Chanos chanos* cultured in saline ponds in Asia.

Cichlidae—*Tilapia mossambica* cultured in saline ponds in Asia and introduced into stream tributary to Salton Sea.

Coregonidae—*Coregonus clupeaformis* introduced into three saline lakes in Saskatchewan.

Invertebrates

Family

Nereidae—*Neanthes succinea* introduced into Salton Sea. *Nereis diversicolor* into Caspian Sea.

Penaeidae—Various species of *Penaeus* cultured in saline ponds in Asia.

Palaemonidae—*Leander squilla* and *L. rectirostris* introduced into Caspian Sea.

Culture of useful animals in ponds could be of greatest utility in mediating any harmful effects of effluents from desalination plants. Possibly, this culture could even be carried out in evaporation ponds and the salt could be marketed along with useful animals such as brine shrimp that would certainly appear, and other animals that might be introduced into such ponds at times when the salinities were suitable. The value of some shrimps or of bait fishes, *e.g.*, the mudsucker, *Gillichthys* spp., in the United States exceeds the value of food fishes that might be raised in such ponds. It would, therefore, be logical to concentrate on their culture to maximize the economic returns. The probable economic returns would no doubt justify some control of salinities in the ponds at less than lethal levels for the fish or shrimp (less than about 70 ppt for *Gillichthys*, Barlow 1961).

The beneficial effects of fertilizing salt-water ponds have been amply demonstrated ,Gross *et al.* 1944; Gross *et al.* 1946; Raymont 1947a; 1947b; 1948; 1949; Marshall and Orr 1948; Pratt 1949; Chimits 1955). Imaginative design of pond systems accordingly should take into consideration the utilization of sewage effluents, both for control of salinity and fertility. Ponds could also be benefited by the heated effluents from coastal electric power stations which use the water for condenser cooling. Shelbourne (1964) suggested that ponds for culture of marine fish could be placed near the outflow from coastal atomic power stations to take advantage of the elevated water temperature. The elevated water temperature would facilitate the desalination processes, and could make possible the culture in the continental United States of fish such as the milkfish which require and thrive in higher temperatures, or it could make possible the culture in northern regions of the United States of desirable fishes such as the Gulf of Mexico sciaenids, which are known to thrive in high temperature-high salinity habitats.

But future work in the introduction of commercially important species should not be limited to areas affected by effluents from desalination plants. Hypersaline and mineral waters occur naturally throughout the world. The success recorded in the few attempts made to introduce commercial species into such waters, and the field studies which have demonstrated the fact that species useful to man can survive in such waters, ought to stimulate further work in this field.

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175

COMPARATIVE EFFICIENCIES OF VAN VEEN AND SMITH-McINTYRE GRAB SAMPLERS AS REVEALED BY MOTION PICTURES

By

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COMPARATIVE EFFICIENCIES OF VAN VEEN AND SMITH-McINTYRE GRAB SAMPLERS AS REVEALED BY MOTION PICTURES

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Abstract. Two commonly used benthos samplers, van Veen and Smith-McIntyre, were tested to detect possible adverse characteristics for sampling epibenthic animals. A strong hydraulic disturbance (shock wave) was formed below the van Veen sampler as it descended through the water toward bottom. In this sampler the shock wave was sufficiently strong to force aside unattached benthic animals as long as 8 cm. The Smith-McIntyre sampler created only a weak, oscillatory shock wave. Available information indicates that, under standard operating procedures, the smaller the screened opening in the top of the sampler's jaws the stronger the shock wave.

Introduction

Since Petersen's (1913) initial quantitative studies of marine macrobenthos, improvements in the efficiency and reliability of sampling instruments have been only modest. Thorson (1957) published an especially informative review of methods of sampling benthos in which he called attention to a hydraulic disturbance, referred to as a shock wave, created in front of many present-day sampling devices during their descent toward the sea bottom. The wave was thought to push aside the small organisms on the sediment surface. This characteristic was first mentioned by Ekman (1933) and Lindroth (1935).

Field Observations

Field operations of a van Veen grab sampler (Thamdrup 1938), manufactured in Denmark, and a Smith-McIntyre grab sampler (Smith and McIntyre 1954), made in Scotland, were observed during the collection of macrobenthos samples in Vineyard Sound, Massachusetts. Both devices sampled an area of 0.1 m². The most favorable conditions for making observations were in shallow water (2–4 m deep) on light-colored sand. Each time the van Veen sampler was lowered and just before contact with the bottom, it appeared to push aside the brown flocculent detritus and fragments of eelgrass (*Zostera*) on the sediment surface. The Smith-McIntyre sampler had a somewhat similar action, but the movement of the detritus appeared to be considerably less than that produced by the van Veen. Inasmuch as the sequence of events occurred so rapidly during the moment immediately before the grab touched bottom, the accuracy of these observations is questionable. Furthermore, the viewing angle from the boat added to the difficulty of seeing exactly the operation of the sampler and its effect on the sediment surface.

Tank Trials

To document accurately the presence or absence of a shock wave and its possible influence on small epibenthic organisms, comparative lowerings of the two samplers were made in a large indoor tank (1.3 by 1.3 by 2.7 m). The tank was filled with water and the bottom covered to a depth of 15 cm with washed pebbles, ½–1 cm in diameter. A 16-mm Bell and Howell movie camera was mounted outside a window in the side of the tank. Film used was Kodachrome II; shutter setting was 64 frames per second. Numerous lights were installed underwater and above the tank to give suitable illumination.

Ping-pong balls of slightly negative buoyancy (specific gravities of 1.03, 1.04, 1.08, and 1.10) were used to represent epibenthic organisms. A group of four to six of these balls was placed on the tank bottom directly below the sampler before each lowering. The samplers were lowered numerous times, and a representative series was photographed. The sketches in Figure 1 were drawn from enlargements of a series of frames selected from the motion picture film. The numbers of balls retrieved, from a total of 50 available, by each sampler during a typical series are summarized as follows: In 10 hauls with a van Veen sampler 11 balls (22%) were retrieved; in 10 hauls with a Smith-McIntyre sampler 48 (96%) were retrieved.

The consistently small catch of ping-pong balls by the van Veen sampler left little doubt that a strong shock wave was created. When the sampler descended to within about 25 cm above bottom, the lighter balls began to move horizontally (Fig. 1–1). Movement was nearly always toward the sides, not the ends, of the sampler (Figs. 1–2). Heavier balls were pushed out later when the sampler touched bottom and shortly thereafter when the jaws were closing (Fig. 1–3 and 1–4). Usually the van Veen sampler enclosed in its jaws, and retrieved, 25% or less of the balls. The Smith-McIntyre produced a relatively minor shock wave (Fig. 1–7 through 1–12) and retrieved nearly all of the balls. When the approaching sampler was 15–20 cm above the substrate, it produced a quiverlike movement of the lighter balls. Also, when the sample was six balls, they were spread over a wider area and an occasional ball was missed. A ball of low specific gravity and located only a few centimeters inside the perimeter of the area sampled appeared to be pushed aside a short distance by a rather weak shock wave.

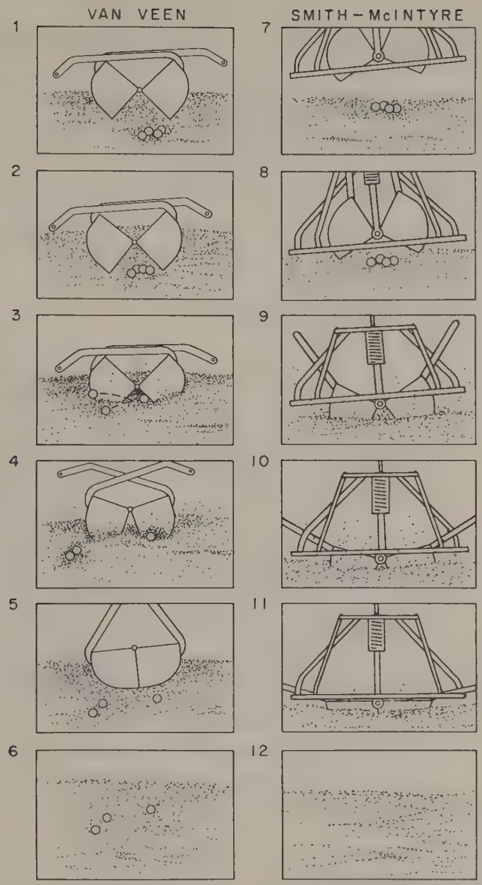

FIG. 1. Sketches from the motion picture film illustrating the influence of the shock wave from van Veen and Smith-McIntyre samplers on lightly weighted ping-pong balls. Note the large proportion of balls pushed aside by the van Veen sampler.

Trials with such items as confetti paper and formalin-preserved invertebrate animals (*Meganyctiphanes,* 3–4 cm long; *Dichelopandalus,* 5–8 cm) substantiated the findings indicated by trials with ping-pong balls. They also verified the contention that unattached epibenthic animals can be washed aside by the descending sampler.

A few concluding trials, in which dye was used, were designed to show the path of water emerging from inside the sampler's jaws while it was descending toward the sea bottom. Crystals of potassium permanganate were placed in tubular cheesecloth bags taped inside the cutting edge of the jaws. When a van Veen sampler thus equipped was lowered to the tank bottom, the dye swirled out the side openings between the jaws. In the Smith-McIntyre sampler, the dye passed upward through the screened opening in the jaw tops.

APPLICATION TO SAMPLING PROBLEMS

The observed results demonstrate that the severity of the shock wave is directly related to the restricted flow of water through the tops of the jaws. Our Smith-McIntyre sampler has a screened opening 14 by 29.5 cm in each jaw, giving a total area of 826 cm^2 for water escapement. Our van Veen sampler has a screened opening totaling only 45 cm^2.

On the basis of these results it is apparent that some grab-type bottom samplers produce an undesirably strong shock wave—a wave sufficiently powerful to push aside macrobenthic organisms at least as long as 8 cm. A sampler that creates a force of this magnitude is unsuitable for many sampling uses. In most grab-type samplers, enlarging the screened openings in the jaw tops would probably reduce the shock wave to minor proportions. An alternative to screened openings would be light-weight hinged plates for jaw tops, similar to those on the Ekman sampler (Welch 1948), which would open on descent and close on ascent. This arrangement might prove more effective than openings covered with metal or plastic screening. The same principle is applicable to the Pettersson sampler (Pettersson 1928) and related types. Also, consideration should be given to an analysis of shock waves in bottom corers that are used for collecting samples of undisturbed sediment.

Interested persons may borrow the motion picture film described above by contacting the Laboratory Director, Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts 02543.

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22. Benthic animals, particularly *Hyalinoecia* (Annelida) and *Ophiomusium* (Echinodermata), in sea-bottom photographs from the continental slope*

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Abstract

Photographs of the sea floor generally have received only partial or superficial use by biologists, largely because of difficulty in identifying the animals. A combined underwater camera and bottom-grab sampler permits fuller use of the photographs.

An analysis of forty photographs of the sea bottom, together with their accompanying quantitative samples of the benthos, revealed a sparse to unexpectedly rich benthic fauna inhabiting the continental slope between Georges Bank and Cape Hatteras.

The polychaete worm *Hyalinoecia tubicola* and the brittle star *Ophiomusium lymani* were the two species shown most commonly and clearly in the photographs; they were also the dominant epibenthic forms in the grab samples. Notes on their size, distribution pattern, body position, tracks, and related ecological information are included in this report.

Large surface-dwelling species comprised a major portion of the total benthic biomass. In both the surface fauna and total benthos, weights and numbers of individuals were largest in the shallowest zone (200 to 500 m) and least in the deepest zone (2,000 to 3,310 m).

A comparison of total benthic biomass (based on grab-sampler data and photographs) clearly indicates that the surface-dwelling component was underestimated using the grab-sampler technique. It is concluded that sea-bottom photographs are a desirable supplement to grab samples in studies of benthic biomass. Furthermore, the photographic method is judged to be superior to the conventional method for determining the biomass of large surface-dwelling organisms.

22–1. Introduction

The number of sea-bottom photographs is increasing rapidly as a result of major technical developments in submarine photography during the past decade (Edgerton, 1963; Shipek, 1960) and substantially increased oceanographic research. Most photographs are not analyzed for their biological content, or are studied only superficially, chiefly because of the inability of biologists to identify the organisms that are disclosed. The rather small size (less than 1 or 2 cm) or thin bodies of many surface-dwelling organisms contribute to the difficulty. Moreover, many animals are partially buried in the sediments or inhabit tubes or cases that frequently leave little, if any, of the body or appendages exposed to view. These factors, the drab coloration that blends with bottom debris, and superficial similarity in appearance of many diverse kinds of organisms (even from different phyla) add to the difficulty of identification of all but a small proportion of the animals.

The identification of animals in photographs is facilitated if a combined camera and bottom sampler are used to collect benthic organisms from approximately the same area of sea floor that is photographed. Such a device was used off southern California by Menzies, Smith, & Emery (1963) and on the continental shelf off New England by Emery, Merrill, & Trumbull (1965). Ideally the sampler recovers many of the same specimens that are photographed. This permits the detailed microscopic examination of the various organisms that generally is necessary for accurate identification.

This report describes the distribution, body positions, tracks, and related ecological aspects of the two principal species of benthic animals in a series of forty photo-

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* WHOI Contribution Number 1761.

Our associates at the Bureau of Commercial Fisheries and the Woods Hole Oceanographic Institution, particularly B. Burns, E. B. Haynes, J. Hulsemann, R. M. Pratt, J. Schlee, R. B. Theroux, and J. V. A. Trumbull assisted in collecting and processing materials; Lowell P. Thomas identified specimens of brittle stars; H. L. Sanders read the manuscript critically; D. M. Owen designed and constructed the photographic unit; and F. A. Bailey prepared the drawing in fig. 22–5. The R/V *Gosnold* was under command of Captain Harry Seibert.

graphs collected with a camera-grab device from the continental slope off the Atlantic coast of the United States. The numerical density and biomass values derived from an analysis of the photographs are compared with those from the grab samples.

22–2. Methods

Equipment

The sampling instrument consisted of a large clam-shell grab with a camera and light attached (fig. 22–1). The basic component was a Campbell bottom grab that covered a bottom area of 0.56 m², had a capacity of 0.20 m³ of sediment, and weighed 250 kg. A Robot Star camera loaded with 35-mm, black-and-white film was mounted in a watertight housing that had an acrylic plastic window in the side. This unit was attached inside one bucket of the grab. In order to compensate for the camera's position offset from the midline it was aimed inward toward the midline at a slight angle to the vertical. The area that was photographed was 0.48 m²; about 72 per cent of this area was encompassed by the jaws of the grab. An electronic flashtube with batteries, condensers, and switching

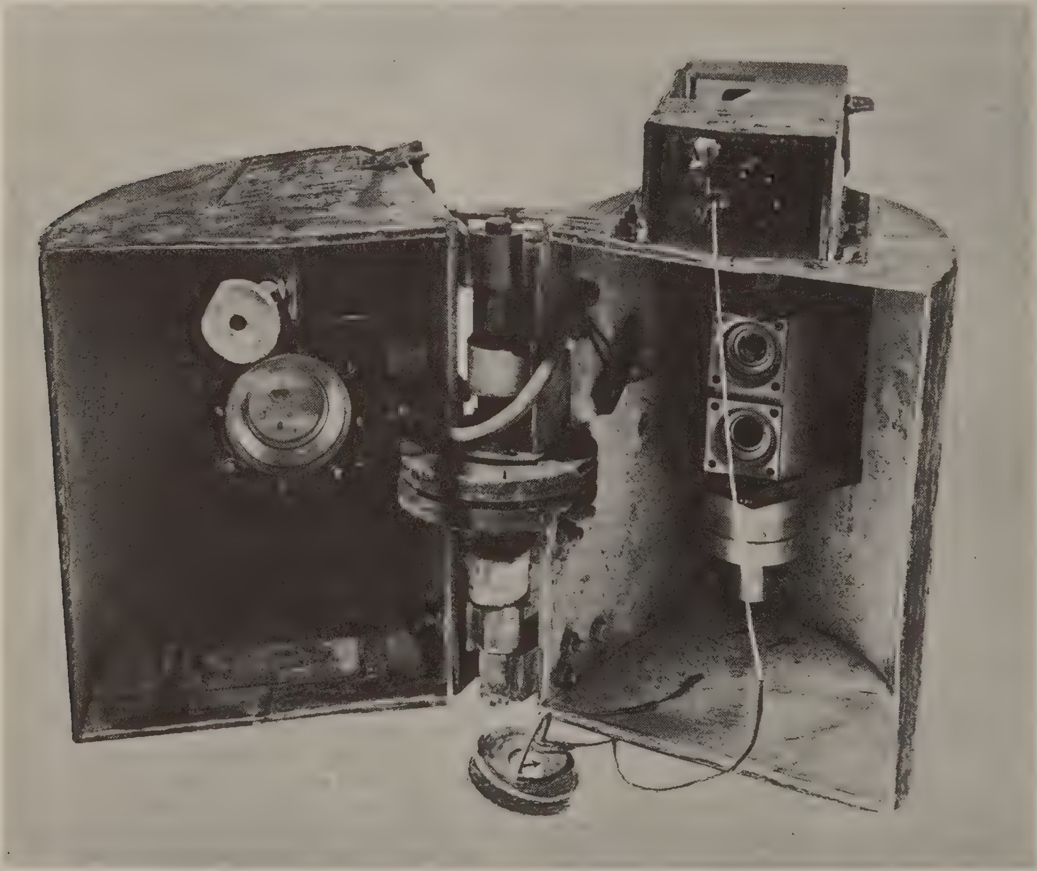

Figure 22–1. Bottom view of Campbell grab sampler and attached camera and high-intensity light. Camera housing is adaptable for stereoscopic equipment. Width of jaws (vertical dimension in photograph) is 57 cm.

solenoid was arranged in a watertight housing attached inside the other bucket of the sampler. The triggering mechanism consisted of a spring-loaded mercury switch and a lead weight suspended about 1 m below the grab.

When the instrument was lowered from the ship, the tripping weight struck bottom first, activating the switch that resulted in film exposure. The sampler continued its descent until it struck bottom, tripped, and enclosed a portion of the sediment and fauna, which was retrieved.

Materials

General. The photographs and bottom samples that form the basis of this report are part of a large series collected by the R/V *Gosnold* in 1963 and 1964 during a survey of the geology and benthic invertebrates of the Atlantic continental shelf and slope (Emery & Schlee, 1963). This survey was sponsored jointly by the U.S. Geological Survey, the Woods Hole Oceanographic Institution, and the U.S. Bureau of Commercial Fisheries. Quantitative samples of the benthos and their accompanying photographs were available from forty stations on the continental slope between Georges Bank and Cape Hatteras (fig. 22–2). Water depths range from 214 to 3,310 m. Bottom sediments are predominantly mixtures of silt and clay, except for those from the upper part of the slope which consist mostly of sand (table 22–1). Geophysical measurements show that these sediments are as thick as 100 m, and that they rest atop Tertiary and Mesozoic shales, marls, and sandstones which are exposed only locally where slopes are especially steep. The continental slope in this region has a general declivity of 2° to 8° (average about 4°).

Processing of samples. At sea the samples were hoisted to the surface and dumped into a large watertight metal box. Several small subsamples of sediment were removed for geological study, after which the remaining material was washed on a 1-mm-mesh screen. All material remaining on the screen (living animals, worm tubes, shell fragments, gravel, etc.) was preserved. The laboratory analysis consisted of sorting the animals into major groups, counting the number of individuals, and weighing each group after excess formalin had been removed by blotting paper. Nonliving components such as gastropod shells inhabited by pagurid crabs, or annelid tubes (whether inhabited or empty) are omitted from the counts and weights. The shells of living mollusks are included in the weight measurements. Portions of individual specimens appearing in the sea-bottom photographs are prorated according to the percentage of the animal showing within the area of the picture. For comparison, all specimen counts are expressed as numbers of individuals per square meter, or grams per square meter (damp weight).

TABLE 22–1. Particle size and composition of sediments in twenty-six bottom samples from the continental slope of the western North Atlantic.[1] (The number of samples upon which each computation is based is shown in parentheses.)

Water depth (m)	Median diameter of particles (μ)[2]	Percentage by dry weight					
		Clay	Silt	Sand	Gravel	Calcium carbonate	Organic carbon
0–500	115	7	21	70	2	6.5	0.51
	(12)	(12)	(12)	(12)	(12)	(12)	(11)
500–1,000	7.5	43	35	22	0	8.6	0.77
	(2)	(2)	(2)	(2)	(2)	(3)	(2)
1,000–2,000	9.1	35	54	11	0	13.9	—
	(6)	(6)	(6)	(6)	(6)	(6)	
>2,000	4.6	48	45	7	0	28.1	—
	(6)	(6)	(6)	(6)	(6)	(10)	

[1] Data on particle size and composition are not available for fourteen of the forty stations from which photographs are described.
[2] Calcium carbonate-free basis.

TABLE 22–2. Number of *Hyalinoecia tubicola* per square meter in photographs or bottom samples on the continental slope of the western North Atlantic.

Station[1]	Water depth (m)	Number per square meter	
		In photo	In grab
1071	346	12	2
2078	365	272	2
1078	376	6	2
2160	400	2	0
1371	446	6	45
1358	450	29	23
1367	455	29	5
1357	564	10	0

[1] Stations are plotted in fig. 22–6. Tracks of *H. tubicola* occurred in photographs from the following stations: 1071, 1078, 1116, 1357, 1358, 1367, 1371, 2074, 2078, 2088, 2099, 2107, 2108, 2152, 2158.

22–3. Organisms in photographs and bottom samples

Hyalinoecia tubicola

One of the largest and commonest organisms appearing in the sea-bottom photographs was the tube-dwelling polychaete worm *Hyalinoecia tubicola* (Müller) — figs. 22–3, 22–4, 22–5. This species appeared in photographs at eight stations distributed from the vicinity of Georges Bank to near Cape Hatteras (table 22–2, fig. 22–6), a wide geographic range that is in keeping with the known cosmopolitan distribution of the species (Pettibone, 1963). Water depths at these stations ranged from 346 to 564 m. This restricted bathymetric range is well within the depth range of this species (274 to 1,170 m) as reported by Verrill (1885) for the western North Atlantic Ocean.

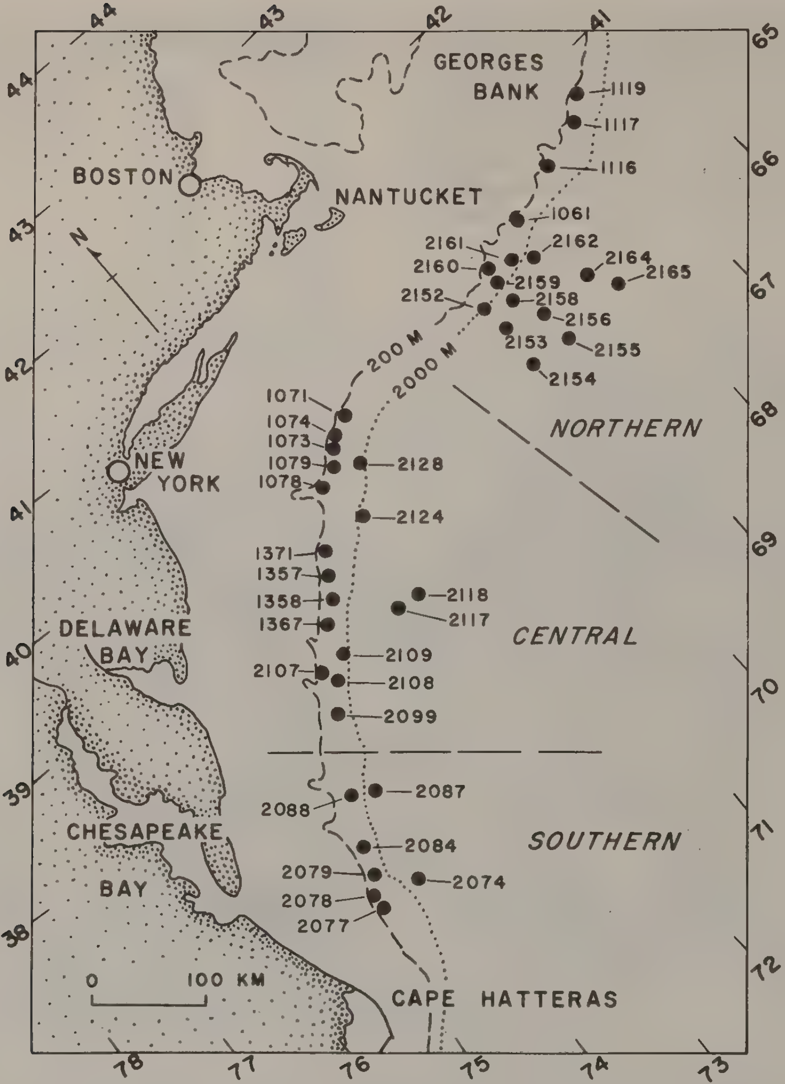
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Figure 22–2. Stations occupied by R/V *Gosnold* on the western North Atlantic continental slope, where quantitative samples of the benthos and clear sea-bottom photographs were obtained during 1963 and 1964. Depth contours are shown for 200 m (broken line) and 2,000 m (dotted line). The region was divided arbitrarily into three geographic regions—northern, central, and southern.

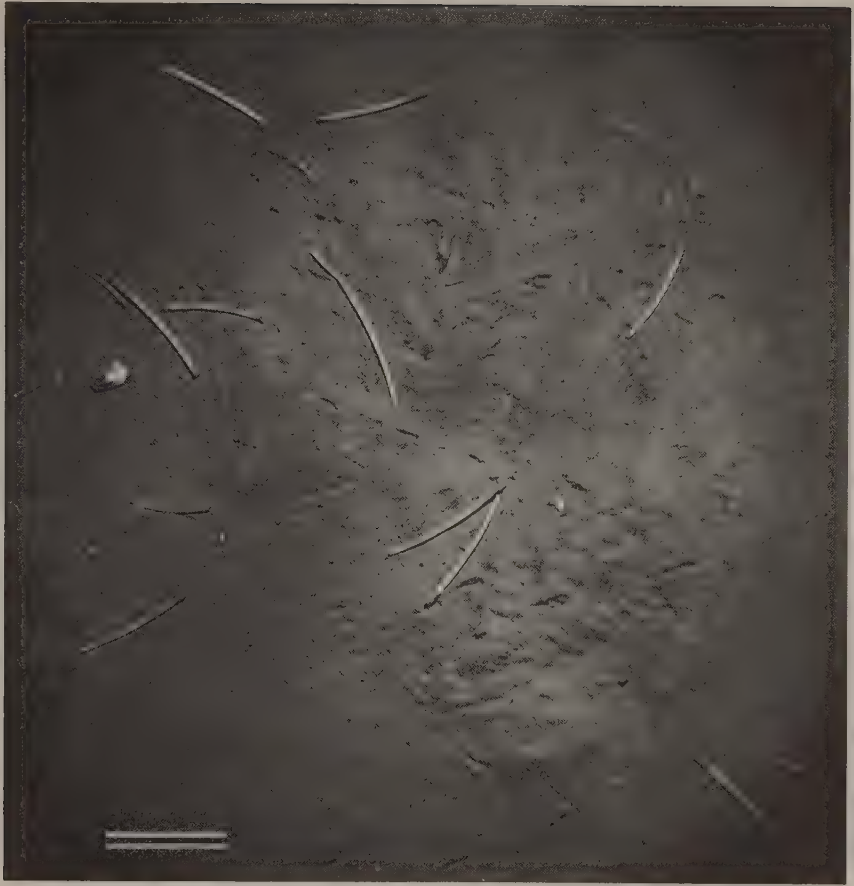


Figure 22–3. Bottom photograph showing *Hyalinoecia tubicola* at Station 1358, east of Delaware Bay (38°42.4′N, 73°01.1′W); water depth 450 m; sediment silty sand. The cloud of suspended sediment at the left-hand side of this and subsequent photographs resulted from the impact of the camera-tripping weight. Scale bar (lower left) is 10 cm.

The depth range for all oceans combined is 13 to 4,380 m (Pettibone, 1963).

The trend of increasing density of worms from the northern part of the study area southward was pronounced (fig. 22–6). The enormous concentration of living specimens at the southernmost station (Station 2078) in this series, illustrated in fig. 22–4, was totally unexpected. Although large numbers of specimens are known to have been taken in trawls dragged along the bottom (Verrill, 1885), the observed density of 272/m^2 is approximately two orders of magnitude larger than expected. Water depth at this location is 365 m, which is not an unusually deep or shallow occurrence for this species.

Bottom photographs showing *Hyalinoecia* have been taken at a depth of 1,935 m on the continental slope off Baja California (Parker, 1963). Their density there was only 1.5/m^2, as compared with the average density of 46/m^2 on the Atlantic continental slope, based on photographs at only those stations where one or more specimens occurred.

Collections and photographs of *H. tubicola* disclosed a high percentage of occupied tubes. An examination of

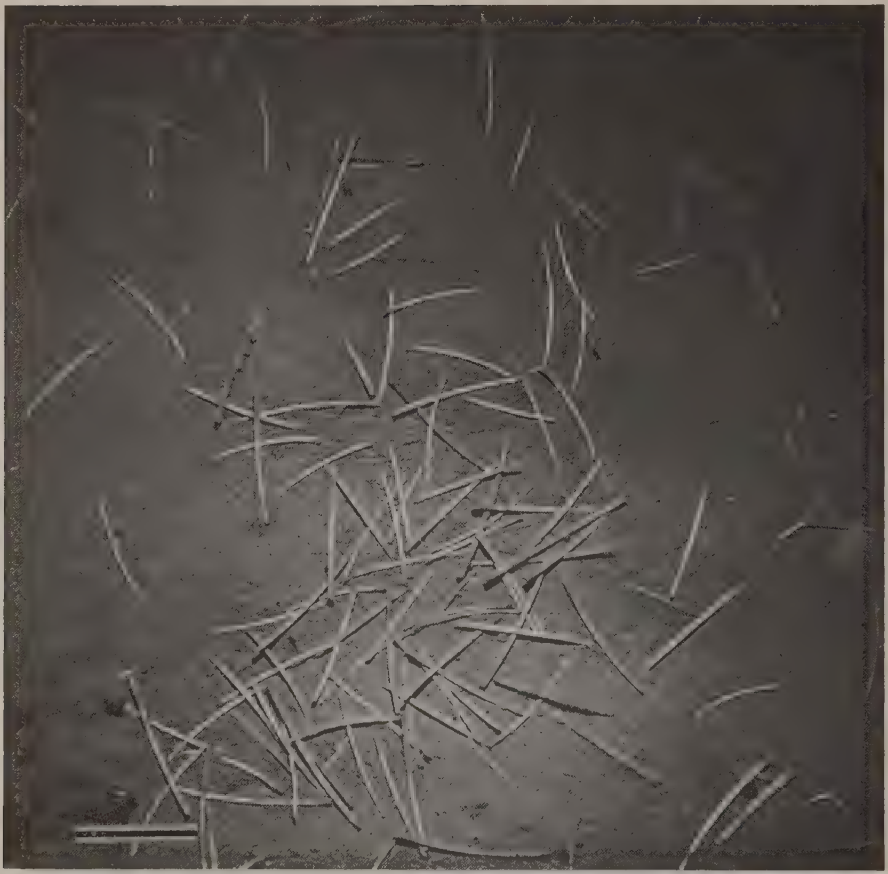


Figure 22–4. Bottom photograph showing *Hyalinoecia tubicola* at Station 2078, southeast of Chesapeake Bay 36°21.7′N, 74°45.3′W); water depth 365 m; sediment foraminiferal silt. Scale bar (lower left) is 10 cm.

the preserved *H. tubicola* from grab-sample collections revealed that 80 per cent of the tubes were inhabited at the time collected. Unoccupied tubes were generally discolored and covered with a detrital film. A considerable number were broken or otherwise incomplete. The tube cavities of a few were completely packed with sediment, suggesting that they may have been buried. Eighty-six per cent of the tubes photographed appeared to be occupied. This value is in general agreement with the ratio observed in the grab samples.

Tube lengths of specimens in the grab samples as well as those in the photographs ranged from 6 to 15 cm, but most were 8 to 12 cm long. The tube gradually tapers from the larger, anterior end (left end in fig. 22–5) to a rather narrow posterior end. Large tubes are nearly straight whereas small ones have a pronounced taper. Diameters at the anterior end are 3 to 8 mm (average, about 5 mm).

Elongate grooves in the sediment that were commonly less than 0.5 cm deep, about 0.5 cm wide, and of lengths reaching to a maximum of roughly 25 cm are present in seven of the eight photographs that depict *Hyalinoecia tubicola*. These grooves appear to be tracks made by the worms as they crawled along the bottom, although this is not a certainty. One reason for doubt is that the tracks rarely appear to be aligned exactly with the worm tubes or to

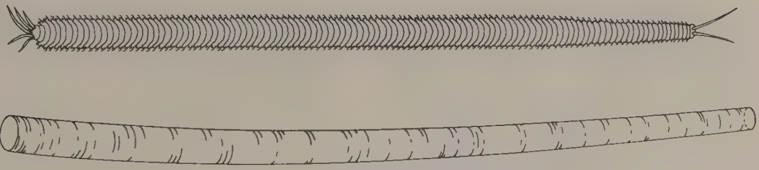


Figure 22–5. Outline drawing of a 10-cm *Hyalinoecia tubicola* and its tube. Drawing by F. A. Bailey.

extend from either the posterior or anterior ends of them. Texture of the sediment and size of the worm would be expected to affect greatly the presence or absence of tracks, and their size. Tracks were present in all photographs showing *H. tubicola*, except at Station 2160. The photograph at this station revealed no tracks, but the sediment was relatively coarse and consequently unlikely to be imprinted. *Hyalinoecia* tracks in the soft sediments of the lower continental slope off Baja California are well illustrated in a report by Parker (1963; plates 14 and 15*b*). In addition to the seven stations where photographs showed both *H. tubicola* worms and tracks, tracks alone are evident in photographs at eight stations. These stations are included in both table 22–2 and fig. 22–6. Their locations are in accord with other information concerning the distribution of this species. General and specific information on distribution, plus the rare and inconsistent occurrence in the grab samples, or photographs, of other species that would be likely to make tracks of this kind, support the conclusion that the sediment markings are tracks of *H. tubicola*.

The photographs record a low level of activity for this species of worm. Only one of the 177 specimens pictured appears to be crawling. Moreover, only about 10 per cent of the worms are partially emerged from their tube. These few are extended one-third or less of the body length from the tube's larger, anterior, end. All emerged worms seem to be exploring the sediment surface, possibly searching for food, but not burrowing or digging deeply in the sediment. A peculiar habit of stacking, in which one worm tube (most often the anterior end) is propped atop another tube like a jackstraw, is clearly shown in fig. 22–4. Absence of detritus along the midline on the upper side of otherwise detritus-covered tubes indicated a scraping action, possibly by lateral movement of one tube along the top of another.

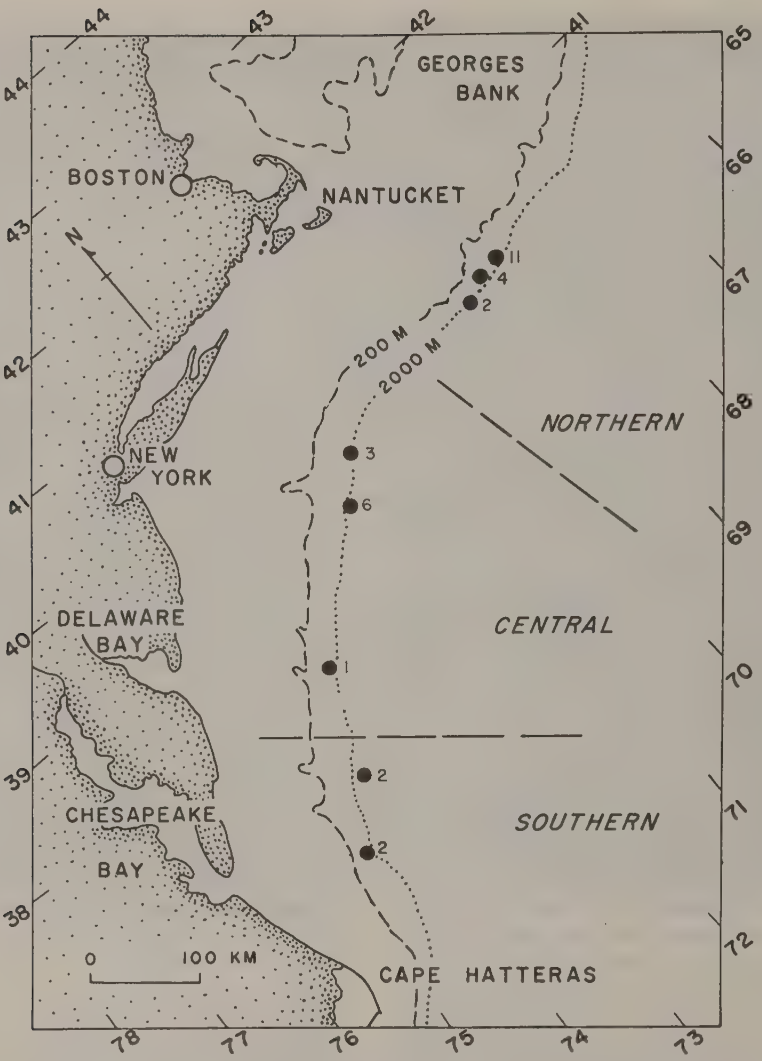
Few large surface-dwelling animals appeared to inhabit the same bottom area with *H. tubicola*. A large-tentacled sea anemone similar to *Bolocera teudiae* was present with the polychaete in two pictures. A 14-cm fish, family Macruridae, is shown swimming in the vicinity of *H. tubicola* in another. It is the only animal photographed or taken in the grab samples that would be a likely predator on this polychaete. A large brittle star, *Ophiomusium*, occurred in four photographs that also included tracks of *H. tubicola*.

A total of 177 specimens are visible in the photographs, whereas only 46 were obtained in the grab samples at these same stations. This ratio suggests that the photographic method is superior to grab-type sampling for determining the occurrence and density of this species. The large size, light color, distinctive shape, and epibenthic habit of *H. tubicola* enhance its detection by photographic means. Without the accompanying grab samples, however, it could not have been determined whether a substantial number of specimens were buried.

Ophiomusium lymani

One of the most handsome and conspicuous creatures in the series of photographs is the brittle star *Ophiomusium lymani* Thompson — figs. 22–7, 22–8, and 22–9. Its large symmetrical form and white coloration contrast sharply with the dark olive-green sediments which it inhabits. Disc diameters of the larger specimens are 1.5 to 2.5 cm, and their arms are 10 to 15 cm long. Because of their large size they were invariably the dominant epibenthic invertebrate species at each station where they occurred. The disc of this brittle star is not circular as it is in many of its relatives, but rather is somewhat pentagonal, with nearly straight margins extending from the insertion of one arm to the next. The long slender arms are commonly straight, except for the distal one-third, which usually is curved upward or sideways.

This species of brittle star appeared in bottom photographs at eight stations (table 22–3). It was distributed from Nantucket southward to near Cape Hatteras, at stations near the base of the continental slope (fig. 22–10). The observed bathymetric range was 1,480 to 2,150 m, an unusually restricted depth interval for deep-water inhabitants of this kind. The depth range reported by Verrill (1885) for collections of this species from the western Atlantic by the *Albatross* was 443 to 3,781 m. The same or similar species occurred in bottom photographs from depths of 1,935 m on the continental slope off Baja California (Parker, 1963).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CHESAPEAKE BAY
CAPE HATTERAS
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11
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Figure 22–6. Distribution and density of *Hyalinoecia tubicola*. Figures to the left of the 200-m contour line give number per square meter, based on analyses of photographs. Stations at which tracks in the sediment made by this species could be seen in the photographs are indicated by the letter *T*.

The average *Ophiomusium* density of 3.9/m² at the eight stations where they occurred (and 0.8/m² if all forty samples are considered) is a substantial number for such large animals, particularly at these great depths. They were somewhat more numerous in samples from the central and northern areas, but this situation may be a vagary of sampling. The unusually high density of 11/m² at Station 2161 (see fig. 22–8) southeast of Nantucket is noteworthy because it represents a large benthic biomass for slope waters. The calculated weight of

TABLE 22–3. Number of large *Ophiomusium* in bottom photographs and in grab samples at eight stations on the continental slope of the western Atlantic.

Station number	Water depth (m)	Number of *Ophiomusium* per square meter	
		In photo	In grab
2159	1,480	4	—
2079	1,545	2	—
2128	1,605	3	—
2161	1,625	11	2
2108	1,660	1	—
2124	1,780	6	2
2152	1,865	2	—
2087	2,150	2	—

Ophiomusium at this station was 31 gm/m². The total benthic biomass for all stations in this region at depths between 1,000 and 2,000 m was 5.9 gm/m², a value determined from grab samples. Wet-weight values expressed here include the skeletal components, which in brittle stars constitute a major share of the total body weight. Even the dry organic weight of *Ophiomusium* at Station 2161 (calculated to be 1 or 2 gm/m²) is a substantial quantity for these depths.

The spacing of individuals varies greatly with their density. Where aggregations were most dense, however, the spacing between individuals is quite regular, seemingly having reached a minimum distance of a few centi-

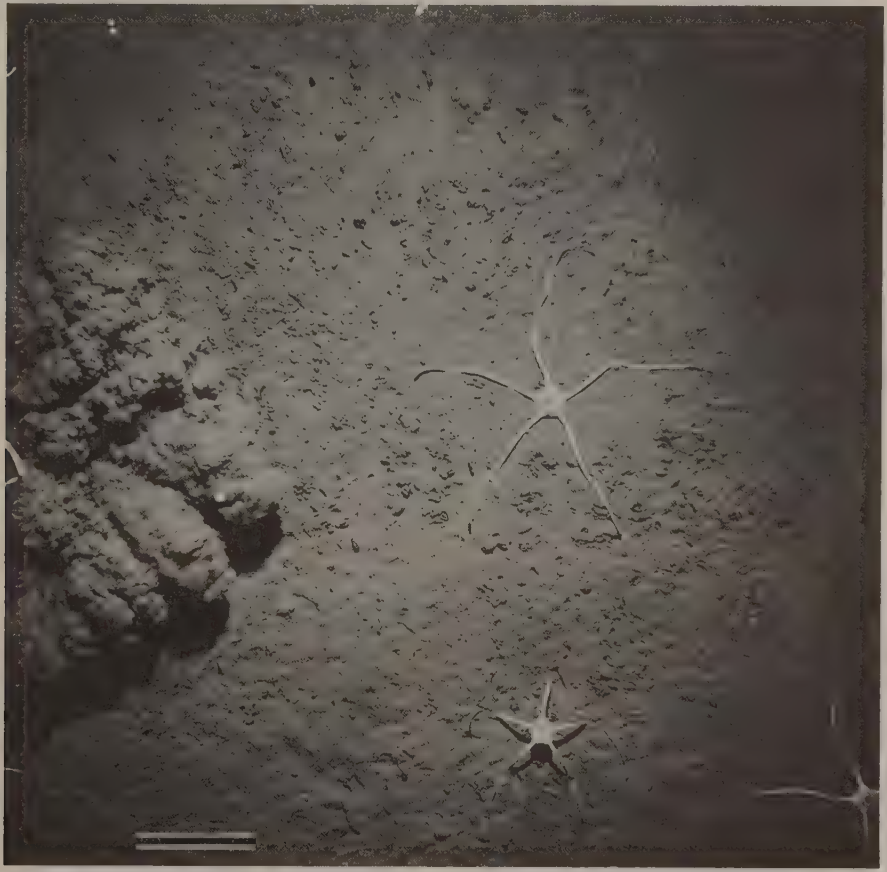


Figure 22–7. Bottom photograph showing the brittle star, *Ophiomusium lymani*, at Station 2124, east of Cape May, New Jersey (30°05.4′N, 72°08.2′W); water depth 1,780 m; sediment clayey silt. Scale bar (lower left) is 10 cm.

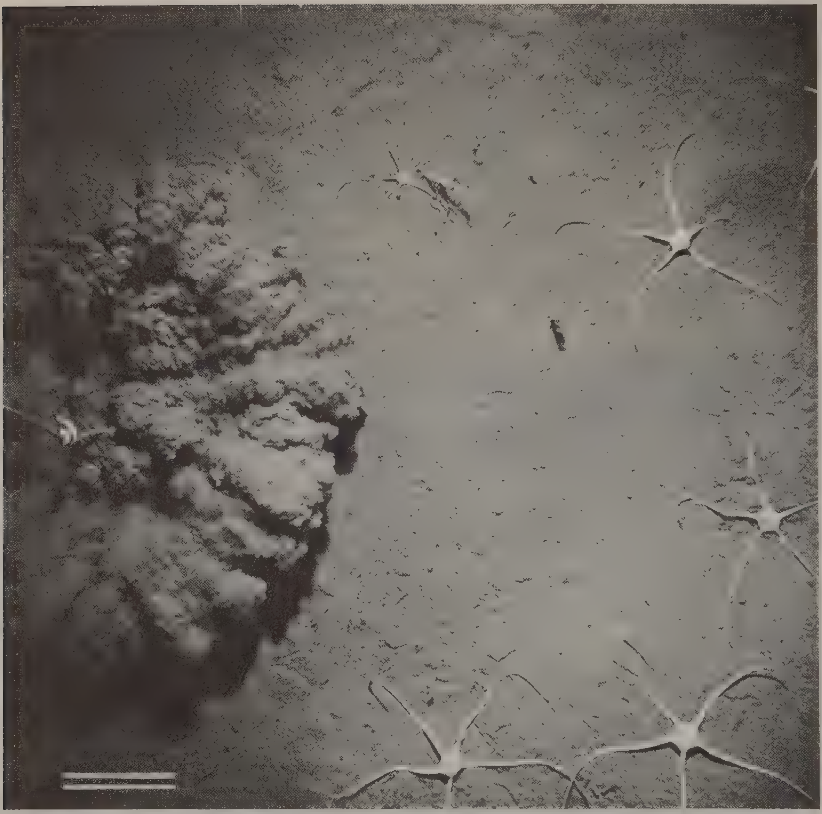


Figure 22–8. Bottom photograph showing the brittle star, *Ophiomusium lymani*, at Station 2161, southeast of Nantucket (39°56.0′N, 68°50.8′W); water depth 1,625 m; sediment clayey silt. Scale bar (lower left) is 10 cm.

meters between arm tips. The overlapping of arms, as seen at the bottom of fig. 22–8, may be a temporary result of the rapid movement of the two specimens toward the right, to avoid the disturbance caused by the camera tripping weight.

When crawling along the bottom, *Ophiomusium lymani* appears to propel itself by a sweeping motion of four arms and trails the fifth arm behind. The direction in which the arms of the specimens are curved in figs. 22–7 and 22–8 suggests that these individuals were moving diagonally from the lower right toward the upper left. Also, the photographs showing more than one individual disclose that the movement of all individuals was in the same direction.

During rapid movements pressure on the sediment is greatest at the middle of the arm or a portion between the middle and the distal quarter (fig. 22–8). On the other hand when movement is slow, the basal three-quarters of the arm leaves an imprint and the arm is pivoted on the sediment about one-half to three-quarters of the distance out from the disc.

Tracks in the sediment surface made by *Ophiomusium lymani* are clearly evident in all photographs that show individuals of this species. Some typical examples are included in figs. 22–7 and 22–8. Tracks in the form of narrow grooves about 0.2 to 0.5 cm wide and commonly less than 5 cm long are representative for this species. The arm tips apparently are not used for body propulsion; presumably their primary function is for tactile and feeding purposes.

Photographic evidence indicates that 80 per cent of the large *Ophiomusium* lie exposed on the sediment surface;

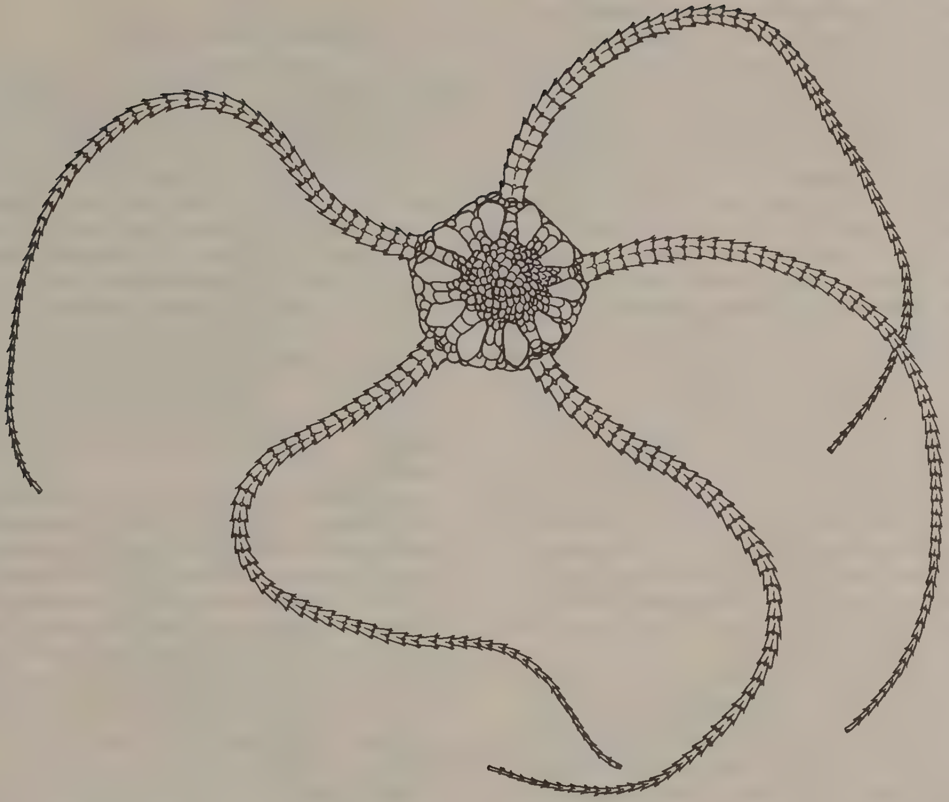


Figure 22–9. Sketch of the dorsal view of *Ophiomusium lymani*. Arm length of this specimen was 10 cm, disc diameter was 1.5 cm.

10 per cent are partially buried in the sediment; and 5 per cent are more deeply buried, with only the arm tips exposed. The remaining 5 per cent have the disc raised several cm above bottom in a peculiar stance. The arms are curved downward from the disc; the midsection of the arms is supported on the sediment and the distal half of the arms is curved upward above the sediment (fig. 22–7).

The proportionately large number of *Ophiomusium* revealed by the photographs compared to the few taken in the grab samples again demonstrated the superiority of the photographic method for determining the occurrence and density of large sedentary epibenthic animals, as compared with the bottom-grab method. Without the supplementary evidence provided by the grab samples, however, the number of specimens buried in the sediment would not be known.

Small brittle stars

In addition to the large *Ophiomusium*, just discussed, small brittle stars were moderately common in the grab samples, and a few were detected in the bottom photographs (table 22–4). The largest included in this category are those with a disc diameter less than 0.5 cm, and arms shorter than 3 cm. Several species were represented in this group, including juvenile *Ophiomusium lymani*. The commonest species appears to be *Amphilepis ingolfiana* Mortensen. All of these small brittle stars have been grouped and treated as a unit because the different species appearing in the photographs cannot be identified.

A total of seventeen small brittle stars appeared in photographs from five stations. Geographically, these stations are distributed from the northern part of the study area to the southern part. Bathymetrically, depths ranged from 214 to 2,910 m. Small brittle stars were not limited to particular depth zones or geographic areas, probably because the several species in this group have somewhat different habitat requirements.

A total of 109 individual specimens of small brittle stars were collected in the forty grab samples (estimated density, 4.9/m²). The density based solely on the photographic evidence was 0.9/m². If only those stations are considered where small brittle stars were detected (in photographs at five stations; in grab samples at twenty-one stations) the average density from the two methods are in close agreement, 7/m² in photographs and 9/m² in grab samples. Individual small brittle stars were not aggregated in clusters, like the large *Ophiomusium*, but were rather widely separated. For example, the photograph taken at Station 2117 (not reproduced here) showed eight individuals. The average distance between them was 12 cm (six arm lengths).

It seems likely that many other small brittle stars were in the bottom areas photographed, but they cannot be seen. This belief is supported by the considerably greater number recovered by the grab sampler (109) than were photographed (17). Some of the grab-caught brittle stars may have been buried in the sediment, but their habit of living on or near the surface suggests that a significant number may have been camouflaged on the sea floor. It must be concluded that the photographic technique is inadequate for quantitative studies of this group of animals.

22–4. Inferences about biomass

How accurate are quantitative estimates of benthic fauna based exclusively upon visual study of sea-bottom photographs? This question is asked more and more frequently as photographic equipment and techniques improve and as the number of bottom photographs increases. It also stems from plans to use underwater manned vehicles, such as *Trieste*, *Alvin*, *Sea-Pup*, and others, for macrobenthic research. In addition, the tedious and expensive process of collecting and processing quantitative samples of benthic fauna is much in need of simplification wherever feasible. Photographic and direct visual methods have been considered as two promising supplements or alternatives to the conventional practice of collecting and studying living or preserved specimens from deep water. The series of photographs and biological samples assembled for this study provides information on some aspects of this subject.

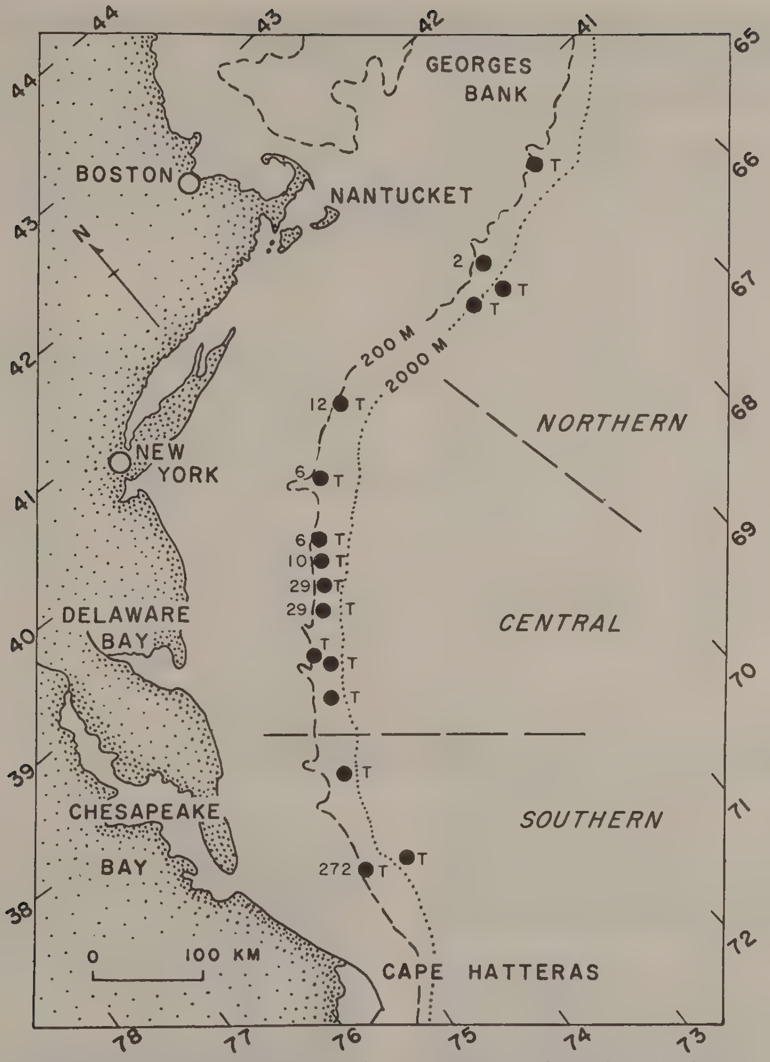
A quantitative comparison was made between contents of grab samples and estimates of the surface-dwelling benthic animals from nearly simultaneous photographs. Without referring to the data from grab samples, the number of living animals in the photographs was counted and the size of each was measured. The weight for individual specimens was derived from measurements of preserved specimens. Mean values for both numbers and weights were determined for northern, central, and southern areas — see fig. 22–2 — and for four water depth zones (200–500 m, 500–1,000 m, 1,000–2,000 m, and greater than 2,000 m). These data, together with comparable values from grab samples, are listed in table 22–5. Each entry is an average of all individual samples in each category.

TABLE 22–4. Number of small brittle stars[1] in bottom photographs and in grab samples at forty stations on the continental slope of the western Atlantic.

		In photographs			In grab samples		
			Number/m² [2]			Number/m² [2]	
Water depth (m)	Number of stations	Number of stations	Average	Range	Number of stations	Average	Range
200– 500	13	2	4	2–6	8	16	2–72
500–1,000	4	0	—	—	3	6	2–11
1,000–2,000	12	1	2	2–2	6	4	2–5
2,000–3,310	11	2	12	8–17	4	8	4–18
200–3,310	40	5	7	2–17	21	9	2–72

[1] *Amphilepsis*, juvenile *Ophiomusium*, and others.

[2] Numbers/m² include only the stations at which small brittle stars were seen (in photographs) or collected (in grab samples).


44
43
42
41
65
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68
69
70
71
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GEORGES
BANK
BOSTON
NANTUCKET
N
2
T
12
200 M
2000 M
NORTHERN
NEW
YORK
6
10
29
29
CENTRAL
DELAWARE
BAY
CHESAPEAKE
BAY
SOUTHERN
272
0
100 KM
CAPE HATTERAS
44
43
42
41
40
39
38
78
77
76
75
74
73

Figure 22–10. Distribution and density of adult *Ophiomusium lymani* in the study area. Density is expressed as the number per square meter, based on the analysis of bottom photographs.

Grab samples disclosed a marked decrease in the total number of individuals per unit area from shallow to deep water and from north to south. The density of specimens along the upper part of the continental slope averaged 302/m², whereas at the base of the slope and beyond, the average density was only 46/m². The decrease in numerical density from north to south was substantial, but considerably less than the depth-related change. Numerical density was roughly two to three times as great in the northern area as in the southern area. Density in the central area was intermediate.

Density of surface-dwelling individuals estimated from

TABLE 22–5. Comparison of total benthos (based on grab-sampler contents) with surface-dwelling benthos (as deduced from photographs). [Values in parentheses are the number of samples on which the computation is based.]

	Epibenthos (photographs)				Total benthos (grab sampler)			
	Water depth (m)				Water depth (m)			
Geographic area	200–500	500–1,000	1,000–2,000	>2,000	200–500	500–1,000	1,000–2,000	>2,000
	Number of individuals per square meter							
Northern	59 (4)	15 (1)	8 (4)	2 (7)	422 (4)	66 (1)	92 (4)	58 (7)
Central	14 (8)	8 (2)	4 (5)	10 (2)	261 (8)	413 (2)	94 (5)	30 (2)
Southern	272 (1)	2 (1)	213 (3)	1 (2)	156 (1)	41 (1)	67 (3)	24 (2)
Average	48	8	58	3	302	233	86	46
	Biomass (gm/m^2)							
Northern	34.2 (4)	69.7 (1)	10.8 (4)	0.3 (7)	8.8 (4)	5.8 (1)	5.8 (4)	[1]3.7 (7)
Central	9.0 (8)	17.9 (2)	4.9 (5)	1.6 (2)	17.4 (8)	8.8 (2)	[2]7.5 (5)	3.7 (2)
Southern	187.2 (1)	1.3 (1)	46.5 (3)	6.2 (2)	10.1 (1)	5.8 (1)	[3]3.3 (3)	3.8 (2)
Average	30.5	26.7	17.3	1.7	14.2	7.3	5.9	3.7

[1] Weight does not include one unusually large specimen; uncorrected weight is 9.3 gm/m^2.

[2] Weight does not include one unusually large specimen; uncorrected weight is 12.5 gm/m^2.

[3] Weight does not include two unusually large specimens; uncorrected weight is 19.6 gm/m^2.

the photographs also revealed a general decrease in number as water depth increased. The densities estimated from photograph analyses were decidedly lower, however, and several were inconsistent with the general trend. The gradient in density from north to south was not evident.

Values of the benthic biomass based on the grab-sampler data are rather consistent in exhibiting a decline in weight with increased water depth. Along the upper part of the continental slope the biomass averaged approximately 14 gm/m^2; at the slope base and deeper it was 3.7 gm/m^2; and at intermediate depths the average generally was between 4 and 9 gm/m^2. There was no apparent trend of decreasing biomass from north to south, as there was for density of individuals. Actually, the central area had a slightly greater weight of benthos than the northern and southern areas.

Biomass of the large surface-dwelling species, based on photographic interpretations, agrees with the grab-sampler results in revealing a marked decrease in benthic biomass at increased water depth. Also, the absence of a latitudinal gradient in weight of epifauna in the photographic analysis corresponds with the grab-sampler results. Principal differences between the biomass values calculated from the two sources are: estimates based on photographs resulted in substantially higher values at all three depth zones shallower than 2,000 m; greater variation in biomass estimates resulted from photograph analyses.

Both the grab and the camera sampled essentially the same fauna, except that infaunal components and small epibenthic animals taken in the sampler were not visible in the photographs. Consequently, the resulting estimates of total benthos weight should equal, or exceed, the weight of the epibenthic component alone. Inasmuch as the estimated epibenthos weight (photographic data) in seventeen of forty samples and in seven of twelve environmental areas (table 22–5) was larger than the total benthos (grab-sampler data), inaccuracies in the sampling techniques are indicated. Gross differences in biomass estimates occurred in only four samples, however, and in each one the grab failed to recover certain specimens that appeared in the photographs. We conclude that sea-bottom photographs are a valuable supplement to grab samples. They are particularly useful in biomass studies in areas where large, distinctly shaped epibenthic species constitute a substantial portion of the macrobenthos. The relative rapidity with which photographic data can be assembled and the broad economic advantage of the photographic method are additional features that favor this method.

22–5. Summary

Bottom samples and sea-bottom photographs were collected with a combined camera and grab sampler at forty stations on the continental slope between Georges Bank and Cape Hatteras. Some quantitative comparisons were made of the photographs and grab samples, and observations were made on the distribution, size, body position, and related ecological aspects of the more common species in the photographs.

Hyalinoecia tubicola, a large tube-dwelling polychaete, was the most common animal in the photographs. A total of 177 specimens appeared in photographs from eight stations. The average density at the eight stations was $46/m^2$; maximum density was an unusually high $272/m^2$. This polychaete occurred along the upper part of the continental slope at 346 to 564 m, from southeast of Nantucket to the vicinity of Cape Hatteras. Elongate grooves in the sediment at fifteen stations were interpreted as tracks of *H. tubicola*. Judging by the few worms protruding from their tube, their activity was at a low level. The stacking of one tube across another was common.

Ophiomusium lymani, a large, handsome, brittle star, was common in photographs taken near the base of the continental slope (1,480 to 2,150 m) between Nantucket and the vicinity of Cape Hatteras. Their density averaged $3.9/m^2$, considering only the stations where they were detected ($0.8/m^2$ at all forty stations), which is high for large animals at these great depths; maximum density was $11/m^2$. This species crawls along the bottom by making lateral sweeping movements with four arms; the fifth arm trails behind. The distal portion of the arm does not appear to be used in locomotion. Spacing between individuals appears rarely to be less than a few centimeters between arm tips. Small brittle stars were common in the grab samples, but only a few were detected in the photographs.

Substantially larger numbers of *Ophiomusium* and *Hyalinoecia* were revealed by the photographs than were captured in the grab. This relationship may demonstrate the superiority of the photographic method over the grab method for determining the occurrence and density of large epibenthic animals. For quantitative studies of infauna and small to medium-sized epibenthic forms (such as small brittle stars) the grab method is better, as discussed in chap. 20.

Benthic animals were most numerous ($302/m^2$) and formed the largest biomass ($14 gm/m^2$) in grab samples from the upper part of the continental slope. They diminished sharply with increased water depth to a density of $46/m^2$ and a weight of $3.7 gm/m^2$ at depths below 2,000 m. The number of individuals in the total benthos, but not the biomass, decreased from north to south at all depths.

A quantitative comparison between grab-sample contents and the fauna estimated from photographs for four depth zones in three geographic areas disclosed similar trends in the estimates of biomass and number of individuals. The comparatively higher biomass estimates from photographic interpretations is attributed chiefly to inefficiency of the grab sampler in collecting the larger animals. Low densities of individuals were relatively lower in the photographs mainly because small epibenthic and infaunal animals could not be detected. The results demonstrate the usefulness of sea-bottom photographs in macrobenthic research, especially in studies dealing with the biomass and ecology of large surface-dwelling species.

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The Standing Crop of Benthic Animals in a North Carolina Estuarine Area

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Benthic organisms are an important part of the biota of shallow estuaries. Although only a few species may be of direct economic value, all form some part of the food web that ultimately sustains commercial fisheries, and are thus of concern in fishery investigations. Despite a long history of taxonomic and ecological investigations of marine benthic fauna of the Beaufort, N. C. area, only one study of standing crop has been made (Brett, 1963) and this limited to infauna containing hard parts likely to be fossilized. During August to November of 1963, benthic fauna were investigated at a single location in Beaufort Harbor to obtain some estimate of the standing crop. Although limited in scope, the study represents the only measurement of the biomass of benthos in a North Carolina estuary.

The area sampled, a gently sloping shore on the west side of Pivers Island, forms part of a shallow embayment about 3 ha. in extent. The embayment consists of mud flats, sand bars, and eel grass beds interspersed with channels up to 4 m. deep. The average tidal range is 0.9 m. During the period of sampling, salinity ranged from 27 to 36‰ and temperature ranged from 15° to 28° C., although the annual ranges in this area are at least from 13 to 36‰, and from 4° to 29° C. (Williams, 1966).

Methods

Ten samples of sediment were taken at each of five elevations. These elevations extended from 0.3 m. below mhw (mean high water) to 1.2 m. below mlw (mean low water) and included sediment types ranging from sand at the highest elevation through bare and eel-grass-covered muddy sand to soft ooze at the lowest elevation (Table I). Each sample consisted of five 71 cm.^{2} cores from 15 to 20 cm. deep. Cores were washed through a screen with openings 6 mm. square, and the organisms separated by hand from the material (mostly broken shell) that the screen retained. This screen retained all organisms weighing 0.2 g. or more, and an undetermined fraction of the smaller organisms. The smaller forms were entangled in the debris on the screen. Organisms were separated into taxonomic groups, counted, and weighed intact after blotting with paper. These live weights, which included inorganic material such as the calcareous portions of shells and the water trapped within body cavities, were multiplied by appropriate factors to convert them to weights of dry tissue. The factors (Table II) were obtained by drying representative species at 105° C. for ca. 24 hr. Prior to drying, mollusks, crustaceans, and echinoderms were decalcified by immersing them in 20% HCl until all hard parts were dissolved. Our factors are similar to those of Petersen (1918) and Petersen and Boysen-Jensen (1911).

Since the distribution of weights and numbers of organisms was highly skewed (with many small and few large values), the data were converted to logarithms (after adding one to each value to eliminate zeros) to help normalize the distribution. Estimates of statistical parameters were transformed back to the original units.

Results and Discussion

The five elevations differed by as much as two orders of magnitude in the average quantity of benthos retained by the 6 mm. screen (Table I). The (arithmetic) average weight and number were least at the highest and lowest elevations and greatest in the eel-grass-covered, sublittoral region (Elevation 4). At all elevations most of the total number and biomass were concentrated in one or a few samples. The individual sample with the greatest number of organisms contained 19 to 48 per cent of the total for its elevation, and the sample with the greatest live weight of organisms, 29 to 89 per cent of the total. Con-

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Table I

Standing crop of benthic animals adjacent to Pivers Island, Beaufort, N. C.

Elevation Number	Distance above mlw (m.)	Sediment	Range of values for 355-cm.^{2} Samples		Number (/m.^{2})			Live Weight (g./m.^{2})			Decalcified Dry Weight (g./m.^{2})		
			Number	Live Weight (g.)	Mean (Arithmetic)	Mean (Log)	Confidence Limits*	Mean (Arithmetic)	Mean (Log)	Confidence Limits*	Mean (Arithmetic)	Mean (Log)	Confidence Limits*
1	0.6	Sand	0-4	0–.64	28	19	3–45	2.6	.51	0–2.0	.28	.06	0–.25
2	0.3	Muddy sand	0–6	0–2.06	90	79	44–130	20	6.5	1.5–27	2.0	.79	.23–3.0
3	0.0	Muddy sand	2–9	<.01–17.48	124	111	75–162	56	2.9	.5–13	5.1	.45	.08–2.1
4	–0.6	Muddy sand with grass	3-115	<.01–40.82	672	371	158–825	294	47	7.6–280	32	5.0	.79–30
5	-1.2	Soft mud	0–6	0-3.48	48	35	11–73	13	3.1	.3–14	1.1	.25	.06–1.1
1–5					192			77			8.1		

*95% confidence limits for the mean of the logarithmic values.

Table II

Dry weight of benthic animals as a percentage of live weight

	Per cent
Crustacean*	
Barnacle	8%
Isopod	16
Decapod	20
Hermit crab (with shell)	5
Mollusk*	
Gastropod	10
Pelecypod	7
Echinoderm*	
Brittle star	10
Sea urchin	8
Tunicate	
Styela plicata	11
Annelid	20

*Decalcified prior to drying.

centrations of weight in individual samples came chiefly from one or a few large organisms, and not from an abundance of small organisms. At all elevations, 10 per cent or fewer of the animals composed over 50 per cent of both total live weight and total decalcified dry weight.

The statistical significance of differences among logarithmic means in Table I was determined by the method of Tukey (Snedecor, 1956, p. 251). The results are summarized below. The lines join elevations with means not significantly different at the 95 per cent confidence level.

	Number	Live weight	Dry weight
Elevation	$\overline{1}\ \overline{\overline{5\ 2}\ \overline{3}}\ 4$	$\overline{1\ 3\ 5\ 2}\ \overline{4}$	$\overline{1\ 5}\ \overline{\overline{3\ 2}\ \overline{4}}$

Although animals were clearly most abundant in the eel grass at Elevation 4 (Table I), animal numbers at other elevations can be considered to form a continuum with no one average significantly different from all others. Differences between the logarithmic averages for both live and decalcified dry weight were significant only for the more widely separated values.

The taxonomic distribution of benthos by number and weight is summarized in Table III. In terms of total weight, the large tunicate, *Styela plicata,* which attached to clumps of eel grass, was the dominant organism, not only for Elevation 4 but for the entire area. *Styela* constituted 89 per cent of both the live and the dry weight at Elevation 4 and approximately 70 per cent of these weights for the entire 50 samples, but only 3 per cent of the population at Elevation 4 and 2 per cent of the entire population. Omitting *Styela,* the benthos were predominantly infauna, mainly mollusks and annelids. The annelids formed the majority of the population at all elevations, and the mollusks the bulk of the biomass at all elevations, except the fourth. Together they composed 90 to 100 per cent of the population, 78 to 100 per cent of the live weight, and 75 to 100 per cent of the decalcified dry weight. The remaining organisms were a variety of small crustaceans (crabs, amphipods, isopods, and barnacles) and two echinoderm species (a brittle star and a sea urchin). In addition to the groups listed in Table III, several others were observed in the samples from Elevation 4, but not enumerated. The eel grass and *Styela* had epiphytic growths of hydroids (mostly Sertularidae) and bryozoans, and there were great numbers of free-living nematodes a millimeter or two long.

Although the estimates of numbers of organisms per square meter (Table I) are very much smaller than most of those in the literature (Sanders, 1956, 1960, 1962), differences in methods preclude exact comparisons. Most of the small benthos passed through the 6-mm. screen, and since small forms normally comprise the majority of the population—e.g., 99 per cent in both Buzzards Bay, Mass. (Sanders, 1960) and Alamitos Bay, Calif. (Reish, 1959) —the actual population at Beaufort may be many times that recorded.

The mean value for biomass—8.1 g. dry tissue/m.^{2} (Table II)—may, on the other hand, approach the true value because the larger benthos form the bulk of the biomass (Holme, 1953; Reish, 1959; Sanders, 1960). This standing crop is similar to the 8.5 g./m.^{2} in Buzzards Bay and the 11.2 g./m.^{2} in the English Channel (Holme, 1953). The weight, 1.8 g. dry tissue/m.^{2}, of invertebrates with hard parts (mollusks, crustaceans, and echinoderms)—see Tables II and III—agrees with Brett's (1963) average value of 1.7 g./m.^{2} for inshore areas near Beaufort. The concentration of biomass in a few animals suggests that more precise measurement of total biomass will require adequate sampling of these relatively scarce large forms, as well as more complete sampling of the small forms.

Table III

Percentage distribution of benthic animals among different taxa

Animal	Number (%) at Each Elevation						Live Weight (%) at Each Elevation						Estimated Decalcified Dry Weight (%) at Each Elevation					
	1	2	3	4	5	1–5	1	2	3	4	5	1–5	1	2	3	4	5	1–5
Annelid[1]	70%	75%	86%	53%	59%	60%	7%	9%	3%	22%	9%	10%	12%	19%	7%	40%	20%	21%
Gastropod[2]	10	19	7	27	0	22	70	54	4	28	0	19	64	55	5	26	0	22
Pelecypod[3]	10	6	2	11	35	10	15	37	88	47	69	65	10	26	84	30	55	51
Crustacean[4]	10	0	5	6	0	5	8	0	5	2	0	3	14	0	4	4	0	3
Echinoderm[5]	0	0	0	<0.5	6	1	0	0	0	1	22	3	0	0	0	<0.5	25	3
Tunicate[6]	0	0	0	3	0	2	0	0	0	89*	0	68*	0	0	0	89*	0	72*

*Omitted in calculating the percentage distribution of the other animal groups.

[1] Species not identified. [2] *Bittium varium*, *Nassarius obsoletus*, *N. vibex*, and other species.

[3] *Atrina* sp., *Chione cancellata*, *Dosinia discus*, *Modiolus demissus*, *Pandora trilineata*, *Solemya velum*. *Tellina versicolor*, and other species. [4] *Balanus* sp., *Cilicea caudata*, *Pagurus longicarpus*, *Sphaeroma quadridentatum*, amphipods, and small crabs. [5] Sea urchin and brittle star. [6] *Styela plicata*.

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DOUGLAS A. WOLFE, Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, N. C. **Accumulation of Fallout Cesium-137 by an Estuarine Clam.**

Rangia cuneata (Lamellibranchia) was collected periodically from six stations on the Trent and Neuse Rivers in eastern North Carolina. Naturally-occurring potassium-40 and fallout cesium-137 were determined by gamma spectroscopy. The cesium-137 content of *Rangia* showed a marked seasonal variation (maximum in May-June; minimum in November-December) which corresponded both in periodicity and amplitude to the well-known seasonality of fallout deposition. The cesium-137 in *Rangia* also was related inversely and non-proportionally to the salinity at the upstream sampling stations. The potassium-40 content of *Rangia* increased linearly less than twofold over the salinity range of 0.1–15 ‰, thereby reflecting the internal regulation of potassium. Cesium-137 was two to three times more concentrated in *Rangia* from nearly freshwater stations than in those from 5–15 ‰ salinity. At salinities greater than about 5 ‰, the cesium-137 in *Rangia* was almost independent of salinity, and averaged about 1.7 pCi./100 g. wet weight of soft tissue.

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An unusually light-shelled form of the scotch bonnet *Phalium granulatum* Born

by

Douglas A. Wolfe

Reprinted from Underwater Naturalist, Bulletin of the
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AN UNUSUALLY LIGHT-SHELLED FORM OF THE SCOTCH BONNET

Phalium Granulataum Born

On May 31, 1966, I collected a scotch bonnet (#681) which was conspicuously lighter than other individuals of the species collected at Beaufort, N. C. The animal was dead and the outer part of the foot and the operculum were missing. The shell had been picked up by a commercial trawler fishing for calico scallops in about 90 feet of water, 25-30 miles south of Beaufort Inlet. A second shell, (#708) very similar to the first, but empty, was recovered from the same trawler the following week.

Both specimens (see plate) are characterized by a thin light shell, a narrow reflected outer lip which is not significantly thickened, and a greatly reduced parietal shield. The base of the columella is covered with pustulose callus, but the parietal wall has no

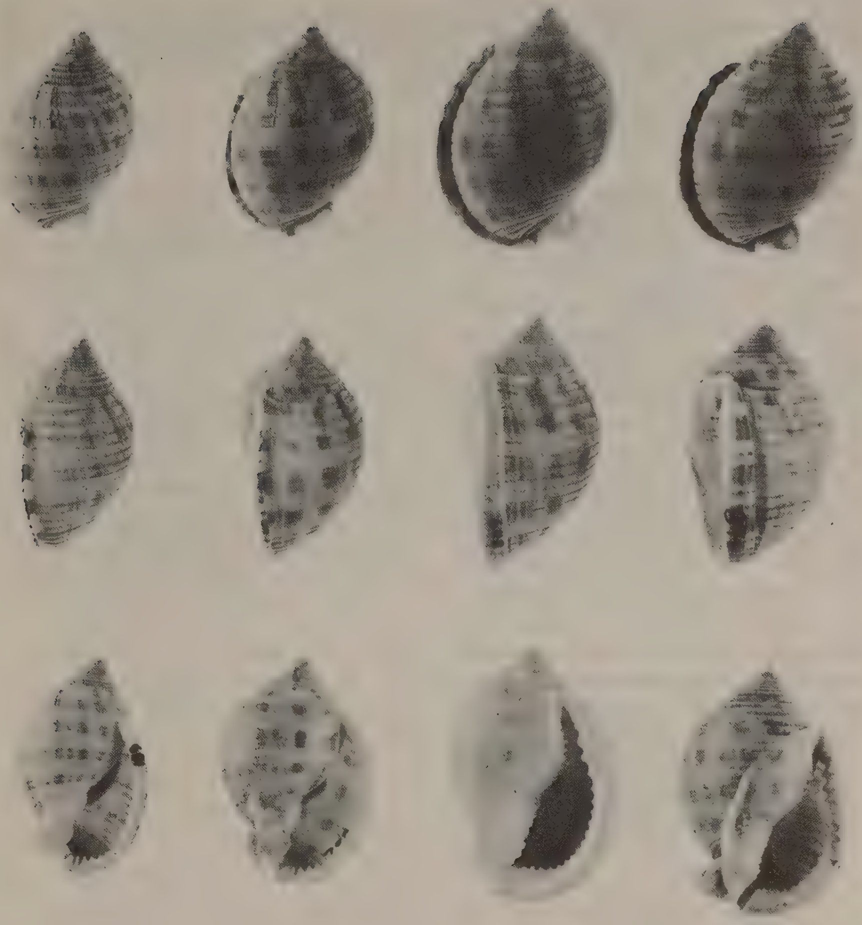

Photo courtesy of author

Thin (on left) and typical shells of Phalium granulatum *Born, all collected from trawlers operating offshore Beaufort, N. C. Actual lengths and weights of the specimens: 49.0 mm., 5.13 g. (#681); 51.0 mm., 6.50 g: (#708) 56.3 mm., 16.92 g. (#648); 55.0 mm., 13.45 g. (846).*

callus and is crossed by the uninterrupted spiral incisions and weak axial riblets which characteristically cover the body whorl of the species. A survey of about 60 other scotch bonnets from the Beaufort region, including several collected on scallop trawlers, revealed one additional shell with these characteristics. The remaining shells, which ranged in size from 40 to 80 mm. in length, had heavy thickened lips and parietal callus with several teeth just inside the aperture. The two individuals from the trawler were outside the 99 percent confidence limit of a least squares regression for the length-weight relationship in the available collection of scotch bonnets. The lengths, maximum diameters, and weights of the two shells were: 49.0

mm., 34.1 mm., 5.13 g. (#681); and 51.0 mm., 35.6 mm., 6.50 g. (#708). The non-conformity of these two individuals with the local population of scotch bonnets led me to believe that they represent a valid subspecies for which I would propose the name *subsolidum*. However, R. T. Abbott has informed me (personal communication) that the light-weight forms are immature specimens of the typical *P. granulatum* Born, and that within a few months of additional development, they would have deposited parietal shields and thickened their outer lips. Abbott further suggested that males are about 30 percent smaller than females when they reach maturity. This fact could explain my finding several "typical" heavy shells smaller than the unusual specimens. I welcome this opportunity to illustrate this one example of the drastic change shells may undergo during molluscan development, especially because these metamorphoses are not emphasized or even mentioned, in the popular shell literature available to shell collectors.

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CASSIS MADAGASCARIENSIS AND C. M. SPINELLA OFFSHORE AT BEAUFORT, NORTH CAROLINA

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According to Abbott (1954. "American Seashells", pp. 193-194), the Caribbean species *Cassis madagascariensis* Lamarck 1822 is replaced in the Florida Keys by the form *spinella* Clench 1944, which is reported to occur also "off Beaufort, North Carolina (fossil?)." Although the helmet shell, previously called *Cassis cameo* Stimpson, has long been known in the state (see for example Dall, 1889. Bulletin of the U.S. National Museum, No. 37, p. 134), Porter (1965. Nautilus *78* (3): 106) only recently confirmed an extant population of *C. m. spinella* off the coast of North Carolina. On September 27, 1966, I collected two live helmet shells from the deck of a trawler loaded with calico scallops, which had been caught some 25 to 30 miles south of Beaufort Inlet in about 90 feet of water. The two helmet shells, catalogued in my personal collection as numbers 1070 and 1071, corresponded clearly to Abbott's descriptions of *C. m. spinella* Clench and *C. madagascariensis* Lamarck, respectively. The two forms, which are represented in my collection also by specimens obtained from the beaches near Cape Lookout, N. C., are readily distinguished. Both have 3 rows of tubercles on the body whorl, but in *C. madagascariensis* Lamarck, the spines are larger and fewer in number, and the size of the topmost spine in the first row of tubercles is exaggerated. In *C. madagascariensis*, the white teeth on the outer lip extend from one-third to one-half the width of the lip and the spaces between the teeth are colored deep brown, whereas in *spinella* Clench the teeth are more restricted to the inner edge of the outer lip and are usually only tinged with brown. The species proper has a generally more massive shell than does *spinella* Clench. Data for the two specimens reported above are shown in the following table:

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[1] The Radiobiological Laboratory is supported through a cooperative agreement between the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.

	#1070 C. m. spinella	#1071 C. madagascariensis
Length, mm.	187	137
Width, mm.	141	106
Number of whorls	9	9
Number of spines in first tubercular row of body whorl	16	10
Number of teeth on outer lip	9	11
Operculum length, mm.	50	35
Operculum width, mm.	6.4	6.7

The presence of *C. m. spinella* Clench off the North Carolina coast is hereby substantiated, and the previously reported range for *C. madagascariensis* Lamarck must be extended northward to include a probable population living offshore near Cape Lookout, N.C. These records, coupled with the report of Warmke and Abbott (1961. "Caribbean Seashells", p. 99) that *C. m. spinella* is found off Puerto Rico, suggest that the two forms of helmet shell occur together over a broad range, extending from North Carolina into the West Indies, as proposed earlier for the species by Dall.—

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MOLLUSCS IN RADIOBIOLOGY AND RADIOECOLOGY

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Research in radiobiology and radioecology is concerned with the behavior of radioactive materials in biological and environmental systems. These fields of study are comparatively new, having developed after the inception of the nuclear age some 25 years ago. It was then that man discovered that the energy in the atom could be released and used--at first for weapons, and more recently for the production of electricity and power to light homes across the country and to drive huge ships across and under the oceans. The major by-products of this power production are radioisotopes--radioactive materials which provide powerful research tools and a useful means in medicine of diagnosing and treating certain ailments. Radioisotopes are produced in quantities much greater than the demand requires, however, thereby giving rise to a waste disposal problem.

The major source of radioactive contamination in our environment has been fallout from nuclear weapons tests. Part of the radioactive by-products of the explosion are injected far up into the atmosphere by the blast. These radioisotopes then slowly settle out onto the surface of the earth as fallout. Waste disposal from nuclear power plants is very carefully controlled, but some radioactivity is nonetheless released into the rivers which supply the water required by the reactors. The radioisotopes, whether from fallout or from reactor effluents, enter the environmental scheme, where they may be cycled continuously through sediments, water, plants, and animals. The Radiobiological Laboratory, located on Pivers Island in Beaufort, N.C., is maintained by the U.S. Fish and Wildlife Service and U.S. Atomic Energy Commission for the study of those processes which affect the distribution and movement of radioisotopes in the estuarine environment and also for the study of the effects of atomic radiation on estuarine organisms. Molluscs, especially bivalves, have played a central role in this research.

Biological Concentration of Chemical Elements and Radioisotopes

Bivalve molluscs are very effective concentrators of chemical elements. Different species accumulate elements to different degrees, and exhibit different anatomical distribution even for the same element. In most instances, the physiological or metabolic explanations for the accumulation are unknown. Notable examples of mineral accumulation by molluscs are the oysters (Crassostrea and Ostrea), the scallops (Aequipecten Pecten, etc.) and freshwater mussels (Unionidae). Oysters concentrate zinc to about 100,000 times the concentration of zinc in sea water. In a typical sea water, therefore, which contains one-millionth of one percent (0.000001%) of zinc, an oyster meat may contain one-tenth of one percent (0.1%) of zinc. This zinc appears to be distributed rather evenly throughout the tissues and organs of the oyster. Similarly, both scallops and freshwater mussels concentrate primarily in the kidney, an organ of excretion, whereas in the mussels the manganese is largely in calcareous tissue whose function seems to be the storage and mobilization of calcium for shell deposition.

If radioisotopes of zinc and manganese are present in the environment, the oysters, scallops, mussels, and other organisms will be unable to distinguish these from non-radioactive forms of the element, and the radioisotopes will be accumulated also. Thus, radioactive zinc and manganese from fallout are presently detectable in shell fish even though their concentrations in sea water are generally too low to measure. Because they have such effective concentrating abilities, these organisms are sometimes considered biological indicators of radioactivity in the environment.

Estuarine Radioecology of Fallout

Molluscs have served as biological indicators to elucidate chemical cycles in the estuary at the mouth of the Trent and Neuse Rivers near New Bern, N.C. The brackish-water clam Rangia cuneata was collected periodically for 18 months from several locations over a 30-mile stretch of the river, and the concentrations of various fallout radioisotopes in the meats of the clams were measured. Several other molluscs occur with Rangia over this area, but they were either too small or too sparsely distributed for routine sampling. Among those other species were: Elliptio complanatus, Anodonta cowperiana, Anodonta imbecilis, and Lampsilis cariosa, all from the fresh water of the Trent River; Polymesoda caroliniana and Congeria leucophaeta from the low salinity waters near the mouth of the Trent River; and Macoma phenax and Macoma balthica from the more brackish waters farther downstream in the Neuse River. The fallout radioactivity in Rangia provided some insight to the general distribution of radioisotopes in the estuary. Nine fallout radioisotopes were detected in Rangia and of these, four (zirconium 95- niobium 95, cerium 141, ruthenium 103, and barium 140-lanthanum 140) appeared suddenly (within 10 days) after the Chinese nuclear tests on May 9 and December 28, 1966. Thus Rangia is a very prompt indicator of new fallout radioactivity in the environment. Differences in the concentration of certain radioisotopes by Rangia from freshwater and brackish water, indicated differences in either environmental concentrations or in the availability of the isotope to the organism in different parts of the estuary. As an illustration of this, ruthenium isotopes were much more concentrated (2-10 times) in Rangia from downstream in the Neuse compared to Rangia from the Trent River. This finding is consistent with the theory that ruthenium, which dissolves in freshwater, becomes insoluble in brackish waters and sea water. Thus the Rangia in downstream samples were probably consuming small particles containing ruthenium with their food, whereas in upstream samples, much of the ruthenium simply flows in solution right by the clams Similar conclusions could be made concerning the distribution of other fallout radioisotopes in the estuary.

Use of Radioisotopes to Determine Feeding Rates of Molluscs

Bivalve molluscs feed on microscopic algae which are filtered from the water pumped through their siphons and across their gills. In experiments conducted at the Radiobiological Laboratory, single-celled algae were reared in the presence of various radioisotopes. The cells containing radioactivity were then placed in aquaria with bivalve such as a quahog (Mercenaria mercenaria). As the clam removed algal cells from the water by filtration, the radioactivity associated with the algae in the water decreased. Thus, the filtering rate of the clam could be learned by following the loss of radioactivity from the water. In this way, the average filtering rate of clams was determined as 5 quarts/hour and that of bay scallops as about 15 quarts/hour. Also by feeding the bivalves different species of radioactive algae and measuring the filtration rates, it was possible to learn something about the feeding selectivity of molluscs.

Radiation Sensitivities of Molluscs

Radiation emitted by radioisotopes has harmful effects when absorbed in sufficient quantities by a living organism. It is important, therefore, to know how much radiation different organisms can successfully tolerate, so that concentrations of radioactivity in the environment can be controlled at safe levels. By irradiating animals with highly radioactive materials under laboratory conditions, it is possible to estimate dangerous doses for different kinds of organisms. In general the more highly evolved forms of life (ultimately man) are most sensitive to radiation. Molluscs successfully tolerate relatively high doses of radiation. For example, when a population of oysters is irradiated with a radiation dose of 150,000-160,000 rads, 50% of the population will die within 30 days. About 110,000 rads is required to kill 50% of a clam (Mercenaria) population in the same time. Only 40,000-50,000 rads kills 50% of a population of mud snails (Nassarius obsoleta) or oyster drills (Urosalpinx cinerea). For means of comparison, the dose required to kill 50% of irradiated white laboratory mice in 30 days is only 400-600 rads. Mammalian systems (including man) are therefore much more sensitive to radiation than are molluscs, and most other marine animals, and it is generally assumed that so long as environmental radioactivity is safe for man, other animals will not be endangered.

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Errata: Page 21, lines 10-15, read: Similarly both scallops and freshwater mussels concentrate manganese to very high levels. In scallops, the manganese is concentrated primarily in the kidney, an organ of excretion, whereas in the mussels the manganese is associated with calcareous tissue whose function seems to be the storage and mobilization of calcium for shell deposition.

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Seasonal Variation of Caesium-137 from Fallout in a Clam, *Rangia cuneata* Gray

In the northern temperate zones, fallout of long lived radionuclides, including caesium-137, varies seasonally, with a maximum during May–June and a minimum during November–December[1]. The concentration of caesium-137 in caribou flesh and in Alaskan Eskimos shows a similar seasonality[2]. Because of its half life of 30 yr and the huge stratospheric reservoir of radioactive debris, the amount of caesium-137 on the surface of the Earth is still increasing, despite the moratorium on atmospheric testing[3]. Although caesium is not a biologically important trace element, chemically it resembles potassium, which is the principal cation of cytoplasm. The bioaccumulation of caesium has therefore aroused considerable interest[4,5]. Whereas the concentration of caesium in marine organisms is usually about three to thirty times higher than in the surrounding water, the concentration for similar organisms in fresh water may be higher by a factor of 100–1,000 (ref. 5). In laboratory experiments with isopods and snails from brackish water, Bryan[6] showed that the biological concentrations of caesium and potassium were directly related and that the concentration factors of both elements were inversely related to the salinity of the water. In the field study reported here, a bivalve mollusc, *Rangia cuneata* Gray, was collected from six stations in the Trent–Neuse estuary in eastern North Carolina (Fig. 1), and the amount of caesium-137 in the soft tissues was measured periodically for 18 months.

The Neuse River drains some 6,000 square miles of the central Piedmont region and coastal plain of North Carolina and receives radioactive pollution only from worldwide fallout. The Trent, a principal tributary, enters the Neuse at New Bern. *Rangia* is collected on a limited scale for human consumption in some estuaries of North Carolina; it is found fairly abundantly on sandy bottoms throughout the sampling area in salinities ranging from $<0{\cdot}1$ to >15 parts per thousand (Fig. 1). *Rangia* were collected at the stations once every 4–6 weeks, the shells were scrubbed and rinsed at the laboratory, and the clams were opened by steaming in a stainless steel bucket on a hotplate. Soft tissues were ashed at 450° C and subjected to gamma-ray spectrometry for analysis of radioactive content[7]. Caesium-137 from fallout and naturally occurring potassium-40 were determined as the sums of the counts comprising their respective photopeaks at 0·662 and 1·46 meV (five 20-keV channels) for a 200-min analysis after correction for background

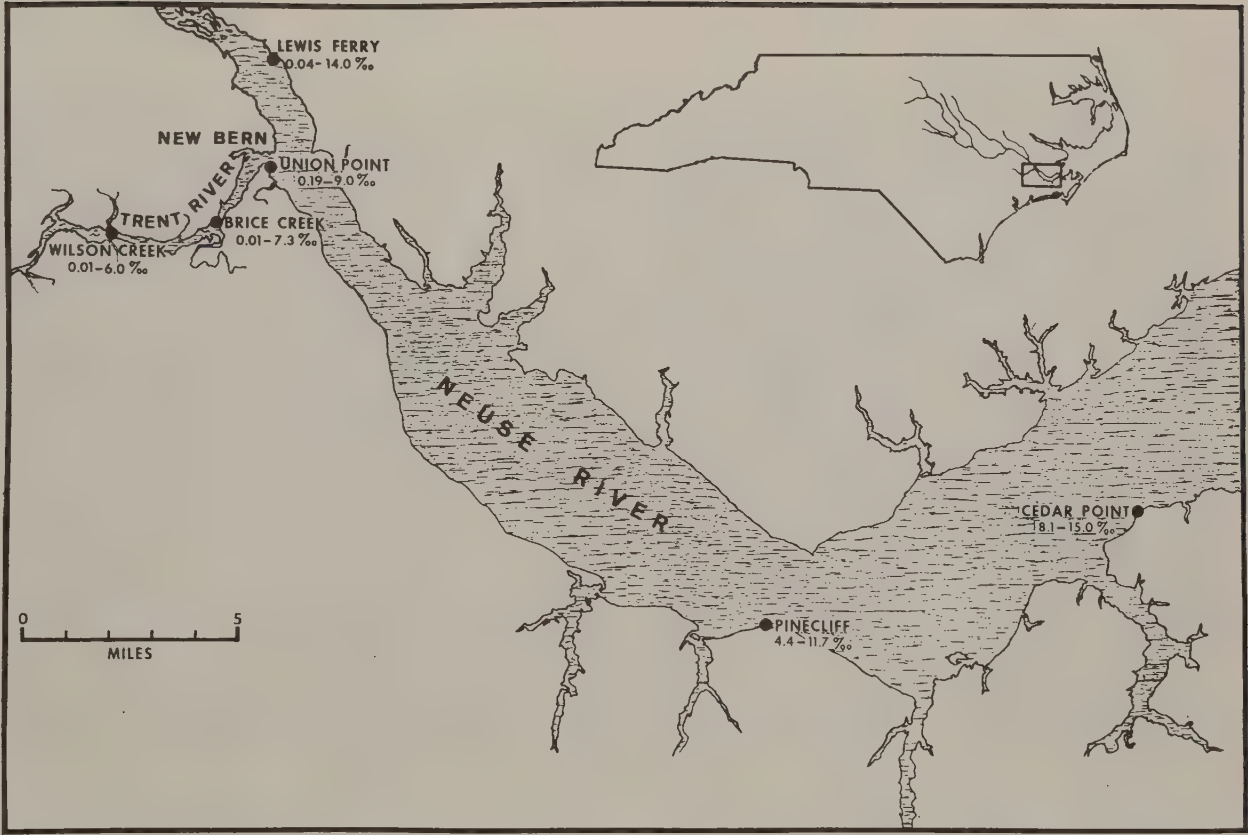
LEWIS FERRY
0.04- 14.0 ‰
NEW BERN
UNION POINT
0.19–9.0 ‰
TRENT
RIVER
BRICE CREEK
0.01–7.3 ‰
WILSON CREEK
0.01–6.0 ‰
NEUSE RIVER
CEDAR POINT
18.1–15.0 ‰
PINECLIFF
4.4–11.7 ‰
0
5
MILES

Fig. 1. Location of sampling stations for *Rangia cuneata* in the lower Trent and Neuse Rivers. Measured extremes of salinity are shown for each station.

and after spectral stripping of other gamma emitting radionuclides[8].

The ratio of caesium-137 to potassium-40 in *Rangia* at the four upstream stations exhibited a pronounced seasonal cycle which was not so apparent in clams from Pinecliff or Cedar Point. The salinity of the water, which was measured coincidentally with the collection of each sample, also varied seasonally, and reflected an inverse relationship to the caesium-137/potassium-40 ratio in *Rangia* (Fig. 2). Although the salinity, and therefore the potassium content, of the water was quite different at the six stations (usually < 1 part per thousand at Wilson and Brice Creeks and 5–15 parts per thousand at Pinecliff and Cedar Point) the concentration of potassium-40

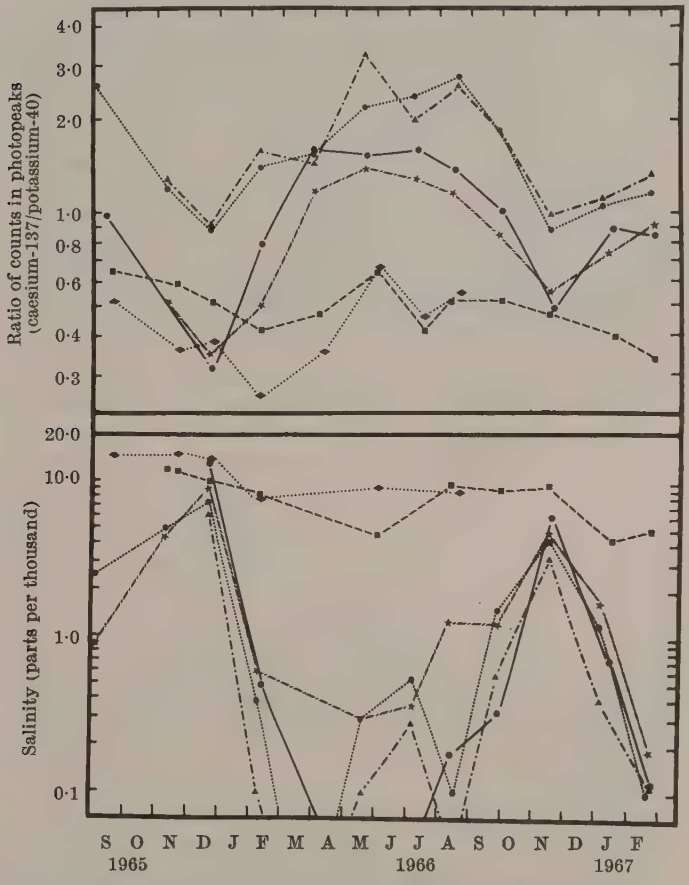

Fig. 2. Variation during 1965–67 of the caesium-137/potassium-40 ratio in *Rangia cuneata* (top) and salinity (bottom) at the stations shown in Fig. 1. Sampling at Cedar Point was discontinued in August 1966 because clams there were relatively scarce. — · —▲—· — ·, Wilson Creek; · · · · ● · · · ·, Brice Creek; —◆—, Lewis Ferry; — - —★— - —, Union Point; – – – ■ – – –, Pinecliff; · · · ◆ · · ·, Cedar Point.

in the tissues of *Rangia* increased only two-fold with salinity (Fig. 3). In Bryan's[6] laboratory experiments, the potassium content of brackish water isopods (*Sphaeroma*) was also stable over a wide range of salinity, and the variability of potassium content at any given salinity was similar to that for *Rangia* (Fig. 3). Because concentrations of potassium are essentially constant, the variation in the ratio of caesium-137 to potassium-40 chiefly represents changes in the concentration of caesium-137 in the clam. In late spring, when the ratio of caesium-137 to potassium-40 attained its highest value at each station, the concentration of caesium-137 in *Rangia* decreased from station to station in a downstream order (Wilson Creek ≈ Brice Creek > Lewis Ferry > Union Point > Pinecliff ≈ Cedar Point). The greatest difference in caesium-137 content between clams from upstream and downstream stations was six- to seven-fold. The absolute activities of caesium-137 in *Rangia* ranged between 0·93 pc. (Cedar Point, February 9, 1966) and 8·33 pc. (Wilson Creek, May 18, 1966)/100 g wet weight, and averaged for all samples 2·79 ± 1·55 pc./100 g wet weight[8].

The seasonal fluctuations of caesium-137 content of *Rangia* may be promoted simultaneously by two phenomena, both of which are correlated with rainfall: (*a*) seasonal variation in the quantities of radioactive debris deposited in the biosphere; and (*b*) seasonal variation in the salinity (potassium content) of the river water at the sampling stations. The variation of caesium-137 in *Rangia* from upstream corresponded closely to the five-

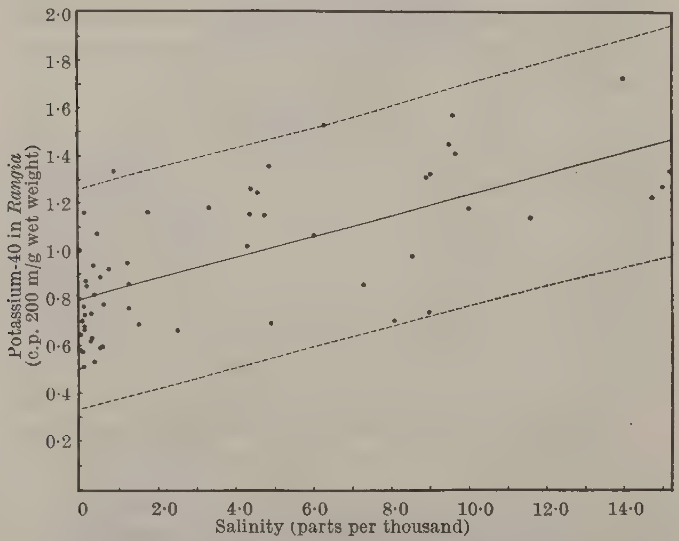

Fig. 3. Least squares regression for the relation of potassium-40 in *Rangia cuneata* to salinity of the water where the clams were collected. Dashed lines are the 95 per cent confidence limits for the regression line.

fold range reported for seasonal variation of atmospheric fallout[1]. The five-fold range of caesium-137 concentration in *Rangia* for a salinity change of more than eighty-fold (from $<0{\cdot}1$ to about 8 parts per thousand at Brice and Wilson Creeks) is not consistent with published results of laboratory experiments. Bryan[9] showed that the concentration of caesium-134 in the crab *Carcinus maenus* is inversely proportional to the concentration of potassium of the water. A similar relationship exists for the concentration of caesium-137 by snails and isopods from various dilutions of sea water[5]. At the nearly freshwater stations in the lower Trent and Neuse Rivers therefore the seasonal variation of caesium-137 in *Rangia* is probably caused principally by fluctuations in the deposition of fallout.

If the concentration of caesium-137 was the same in the water at all stations, the concentrations of caesium-137 in *Rangia* at Wilson Creek might be expected to be much higher in relation to those at Cedar Point than were observed. I therefore surmise that the concentration of caesium-137 is much lower in the fresh water of the Trent River than in the estuarine waters of the Neuse, and that this difference accounts for the lack of inverse proportionality between salinity and caesium-137 in *Rangia* at any one sampling time. Because the bioaccumulation of caesium-137 is influenced by the content of potassium in the water, however, estimates of potential concentrations of radiocaesium in estuarine organisms should allow for seasonal and perhaps even tidal variations in salinity.

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Liquid Scintillation and Geiger Counting Efficiencies for Carbon-14 Incorporated by Marine Phytoplankton in Productivity Measurements

By

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C^{14}-labelled phytoplankton on filter papers were counted with a gas-flow geiger counter, then combusted in oxygen combustion flasks. $C^{14}O_2$ was recovered with hyamine, and the absolute activities of the original samples were determined by liquid scintillation counting. Geiger counting efficiency, based on the absolute activities, was 25·8 % ± 1·19. Intact filter papers containing C^{14}-phytoplankton also were counted directly by liquid scintillation. Comparison of liquid scintillation and geiger activities for the same samples showed that the absolute activity of C^{14}-phytoplankton on filter paper can be determined by direct liquid scintillation counting of the intact sample.

Introduction

The estimation of primary production of organic matter by marine phytoplankton by the C^{14} method (STEEMANN-NIELSEN, 1952) involves incubating phytoplankton for a known time in seawater containing $NaHC^{14}O_3$, filtering the plankton from the water, and subsequently determining the C^{14} in the organisms on the filter paper. Primary productivity, as the amount of carbon fixed per unit time, is then estimated from the total available CO_2 in the incubation medium and the ratio of fixed C^{14} to available C^{14}. The total CO_2 content of ocean water can be determined conveniently, but accurate measures of fixed C^{14} and available C^{14} are more difficult. The C^{14} must be measured either with identical efficiencies or with well-defined efficiencies so that absolute activities can be compared.

Geiger counters have been used most frequently for measuring fixed and available C^{14}. Phytoplankton containing fixed C^{14} are counted on filter papers in amounts generally assumed to be zero thickness, *i.e.* with no self-absorption.

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It is therefore necessary to count the added $NaHC^{14}O_3$ under conditions of zero thickness with identical counting geometry. This determination involves the preparation of $BaC^{14}O_3$ precipitates of varying thickness and extrapolation of the measured activities to zero thickness. Because it is difficult to prepare extremely thin precipitates of $BaC^{14}O_3$ for the usual linear extrapolation (Steemann-Nielsen, 1952; Thomas, 1959), the extrapolations have been made with the assumption of either an exponential function (Jitts, 1957) or a hyperbolic function (Hendler, 1959). Self-absorption, however, probably follows neither an exponential nor hyperbolic function (Jitts, 1961; Jitts and Scott, 1961).

To avoid the complications encountered with $BaC^{14}O_3$, Jitts and Scott (1961) determined the efficiency of their windowless gas-flow geiger counter by counting thin (zero-thickness) films of C^{14}-plastic layered on Millipore filters, which were subsequently dissolved and recounted by liquid scintillation for determination of absolute activity. Saunders, Trama, and Bachmann (1962), however, demonstrated, by using yeast previously incubated with C^{14}-glucose, that cells counted on Millipore filters gave only 83·8% of the activity of cells counted directly on aluminum planchets. This loss of activity was attributed to an absorbing effect of the filter paper, and probably arose from reduced backscatter. Such an effect decreases the likelihood that the geiger counting efficiencies for C^{14}-phytoplankton and the C^{14}-plastic films used by Jitts and Scott (1961) would be identical and re-emphasizes the need for an accurate method to determine geiger counting efficiencies for C^{14}-phytoplankton on filter papers (Doty, Jitts, Koblentz-Mishke and Saijo, 1965).

In this paper, we report the measurement of absolute activities of C^{14}-phytoplankton on filter papers directly by liquid scintillation counting of $C^{14}O_2$ recovered from combusted filters. This procedure permits a precise determination of geiger efficiency if the filter papers are counted with a geiger counter before combustion. We also determine the liquid scintillation counting efficiency for C^{14}-phytoplankton on intact filter papers, and suggest that liquid scintillation is a convenient and reliable substitute for geiger counting in productivity studies.

Methods and Materials

Determination of geiger activity

Geiger counts were made with a Nuclear-Chicago[1] model 1063 anticoincidence gas-flow geiger counter equipped with a Micromil window of less than 150 μg/cm² density. The detector was housed in a model C-115 low background automatic sample changer, and the model 161A scaler was connected to a model C-111 Clary time-interval printer. Matheson Q-gas was used with the flow counter.

The C^{14}-phytoplankton samples used in this study were obtained on the EQUALANT cruises of the International Cooperative Investigations of the Tropical Atlantic (ICITA). Phytoplankton cells on Millipore filter papers were counted repeatedly in aluminum planchets to 2,560 counts. Activities were standardized to a C^{14} reference and corrected for background.

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[1] Trade names referred to in this publication do not imply endorsement.

Combustion of filter papers

After counting with the gas-flow geiger counter was completed, the filter papers were combusted in a modified Thomas-Ogg apparatus similar to that described by Oliverio, Denham, and Davidson (1962). A 2 l filter flask, the side arm closed by an eyedropper bulb, was flushed with oxygen and closed with a rubber stopper from which the Millipore filter paper sample was suspended on a nichrome wire holder embedded in a glass rod. The sample was ignited with an external infra-red heat source. Completeness of combustion and recovery of activity were sporadic when filter papers alone were ignited. To increase the efficiency of combustion, the filter paper was sandwiched between two waxed papers (interleaves commercially packed with Millipore filters). This measure reduced the explosiveness of the combustion and improved the recovery of soluble activity. Immediately after combustion, 10 ml ofhyamine solution (Packard hydroxide of hyamine 10-X; 1 molar in methanol) were injected by hypodermic syringe through the eyedropper bulb on the side arm. The flask was rotated so that nearly all the inside surface was in contact with the trapping agent, and was allowed to stand about 2 hours with occasional rotation and agitation. Duplicate 2-ml aliquots of the hyamine solution were then withdrawn from the combustion flasks for liquid scintillation counting.

Liquid scintillation counting

All samples were counted with a Packard Tri-Carb automatic spectrometer (series 314E) at 0°C. Aliquots of the hyamine solution withdrawn from the combustion flasks were placed in counting vials containing 1 ml absolute ethanol and 10 ml phosphor solution (5 g/l 2,5 diphenyl-oxazole (PPO) and 300 mg/l phenyl-oxazole-phenyl-oxazole-phenyl (POPOP) in toluene). Phytoplankton labelled with C^{14} were also counted by covering the intact filter paper in a vial with 10 ml of the above phosphor solution, thereby rendering the filter paper transparent. After the samples were counted at least 3 times for 3 minutes each, 100 µl of internal standard C^{14}-toluene (Packard, Catalogue No. 6004062) with an absolute activity of 6,710 DPM were added to each vial and the samples were recounted in the same way. The counts from the samples were corrected for background, and the absolute activities of the original filter papers were determined from the counting efficiencies calculated for the internal standard in each vial.

Efficiency of Gas-Flow Geiger Counter for C^{14}-Phytoplankton on Filters

A series of 15 phytoplankton samples on filter papers was counted 5–8 times with the geiger counter, and the filters were then combusted and counted by liquid scintillation (Table 1). Variation of the counting efficiencies of the added internal standard from 29·4 to 44·0% indicated variable amounts of quenching in the samples. The lower values were obtained consistently in samples that were noticeably coloured. Internal standards alone were counted with an efficiency of 69·7%. The absolute activity of each sample, calculated from the individual counting efficiency for each vial, was compared to the original geiger count to determine the efficiency of the geiger counter (Table 1). Average geiger efficiency was 25·8 ± 1·2% (standard deviation).

Liquid scintillation counting is a reliable means of determining the absolute activity of dissolved C^{14}, because the counting efficiency is readily determined with an internal standard. The precision of liquid scintillation counting of

Table 1

Geiger efficiency for C^{14}-phytoplankton on filters[1]

Filter No.	Liquid scintillation		Absolute activity DMP	Geiger CPM	Geiger efficiency (%)
	CPM	Efficiency (%)			
78 A	171	29·4	2,856	792	27·7
B	166	29·6			
98 A	276	41·1	3,296	853	25·9
B	273	42·2			
102 A	1,877	42·7	22,300	5,330	23·9
B	1,861	41·1			
104 A	314	41·0	3,670	874	23·8
B	302	43·0			
106 A	1,101	41·6	13,160	3,365	25·6
B	1,102	42·1			
108 A	695	43·4	8,048	2,148	26·7
B	686	42·4			
112 A	923	42·3	11,060	2,810	25·4
B	920	41·0			
114 A	399	41·6	4,844	1,310	27·0
B	406	41·5			
116 A	864	41·6	10,690	2,810	26·3
B	880	40·0			
118 A	750	42·3	8,928	2,389	26·8
B	766	42·6			
122 A	828	41·9	9,725	2,557	26·3
B	802	41·9			
124 A	1,141	42·0	13,820	3,707	26·8
B	1,187	42·6			
C	1,153	42·7			
D	1,186	41·5			
128 A	1,623	43·5	18,830	4,920	26·1
B	1,646	43·8			
C	1,620	42·3			
D	1,650	44·0			
138 A	1,206	36·4	16,790	4,126	24·6
B	1,202	36·7			
C	1,230	34·8			
D	1,194	36·1			
142 A	1,375	42·2	15,630	3,793	24·3
B	1,336	43·0			
C	1,339	43·6			
D	1,335	43·5			
					Mean: 25·8
					SD: 1·19

$C^{14}O_2$ recovered from combusted C^{14}-phytoplankton on filter paper is reflected in the standard deviation of 1·19, which is only 4·6% of the mean geiger efficiency calculated from the absolute activities of the samples (Table 1). This figure compares favourably with the standard deviation of 5·8% of the mean geiger efficiency obtained by JITTS and SCOTT (1961) using C^{14}-plastic films. Our method has the advantage of determining the efficiency for the particular conditions of geometry, self-absorption, backscatter, etc., encountered specifically with C^{14}-phytoplankton on filter papers prepared for productivity measurements. Attempts to duplicate these conditions with a separate C^{14}-labelled material are unnecessary.

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[1] The mean liquid scintillation cpm are shown for duplicate (A and B) or quadruplicate 2 ml aliquots of hyamine solution. The absolute activities are average values for the aliquots, multiplied by 5 to represent the entire original filters.

Table 2

Liquid scintillation counting of C^{14}-phytoplankton on intact filters

Filter	Liquid scintillation			Geiger	
No.	CPM	Efficiency (%)	DPM[1]	DPM[2]	DPM[1]/DPM[2]
270	1,152	70·0	1,645	1,571	1·05
272	7,690	67·6	11,370	10,480	1·08
274	3,352	68·3	4,907	4,641	1·06
276	6,721	65·8	10,210	9,248	1·10
278	8,823	68·0	12,970	12,410	1·05
280	1,621	69·6	2,329	2,190	1·06
282	7,211	68·8	10,480	9,931	1·06
284	4,497	69·4	6,479	6,548	0·99
286	6,696	67·4	9,934	9,529	1·04
288	8,616	68·6	12,560	12,250	1·03
290	1,314	68·7	1,912	1,866	1·02
292	12,680	65·2	19.440	17,810	1·09
294	4,651	67·8	6,859	6,932	0·99
296	8,814	69·6	12,660	13,110	0·97
298	7,825	68·4	11,440	11,100	1·03
300	1,202	69·3	1,734	1,777	0·98
310	4,020	68·9	5,834	5,386	1·08
320	2,745	68·7	3,995	3,635	1·10
324	2,784	69·6	4,000	4,169	0.96
330	2,993	66·7	4,487	4,025	1·11
338	13,560	68·0	19,940	20,080	0·99
340	2,664	69·1	3,855	3,607	1·07
344	10,450	66·0	15,830	14,300	1·11
350	1,613	69·4	2,324	2,380	0·98
	Mean:	68·3		Mean:	1·04
	SD:	1·3		SD:	0·047

The accuracy of any determination of absolute activity by liquid scintillation counting depends upon the accuracy of the absolute activity of the internal standard. For example, the variations in pipetting the C^{14}-toluene and in making replicate counts result in a standard deviation of only 1·9% of the mean efficiency of 68·3% for counting the added internal standard (Table 2), whereas the stated accuracy of the standard was ± 2·17%. For purposes of comparison, a second reference standard (hexadecane-1-C^{14}, Radiochemical Centre, Amersham, code CFR 5) with a stated standard deviation in activity of less than 2% was counted in the same solvent system with a calculated efficiency of 71·3% This second standard was not used in any of the calculations, but the difference in counting efficiencies based on the two standards helps to demonstrate the limits of accuracy in the liquid scintillation method.

The accuracy of the geiger efficiency determined is also influenced by the possibility that recovery of combusted C^{14} by the hyamine solution is not quantitative. Kelley, Peets, Gordon and Buyske (1961) reported for a similar procedure recoveries greater than 98% for dry biological samples. Quantitative absorption of $C^{14}O_2$ from combustion flasks has also been obtained (Woeller, 1961; Oliverio et al., 1962) using phenethylamine as the absorbent. We found no satisfactory method for determining recovery of C^{14} from combusted phytoplankton because the absolute activities of the samples were unknown. When liquid scintillation counts of combusted filter papers were compared

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[1] Calculated using the efficiency for the liquid scintillation internal standard.

[2] Calculated from the geiger counts and the previously calculated geiger efficiency of 25.8%.

Table 3

Recovery of C^{14} from combusted phytoplankton

	Liquid scintillation DPM geiger cpm
Combusted filters[1]	3·85 ± ·046 SE (15)
Intact filters[1]	4.10 ± ·172 SE (13)

$$\text{Recovery} = \frac{3{\cdot}85}{4{\cdot}10} = 93{\cdot}9 \pm 4{\cdot}1\,\%\ (\text{SE})$$

with liquid scintillation counts of 13 filter papers dissolved in 5 ml of dimethyl formamide and 10 ml of phosphor solution, a recovery of about 94% from the combustion procedure was indicated (Table 3). The liquid scintillation activities of samples containing dimethyl formamide were unstable, however, and decreased during the time between the first count and the count with the internal standard. A correction for this decrease gave a recovery of over 100%. We have therefore considered 94% a minimum recovery for the method. Digestion of the filter paper and phytoplankton in aqueous sodium hydroxide and subsequent liquid scintillation counting of the suspended digest (Tye and Engel, 1965) may provide the means for determining the absolute activities of the samples, and thereby, the recovery from the combustion procedure. No correction for recovery has been applied to the data in this paper.

Liquid Scintillation Counting of Intact C^{14}-Phytoplankton on Filters

Twenty-four filter papers containing C^{14}-phytoplankton were placed in scintillation vials, covered with 10 ml volumes of phosphor solution, and counted by liquid scintillation. The absolute activities of the filters were determined from the counting efficiency of the added internal standard, and these activities were compared with the absolute activities calculated for each sample from the geiger activity and the previously determined geiger efficiency of 25·8% (Table 2). The mean ratio of absolute activities calculated by the two methods was 1·04 ± 0·047 (SD). The absolute activity of particulate C^{14}-phytoplankton counted on a filter paper in the bottom of a vial can therefore be determined precisely from the counting efficiency of the added C^{14}-toluene. The advantages of scintillation counting of particulate matter on intact filter papers were discussed by Funt and Hetherington (1960), although the counting efficiency of their system for C^{14} was only 31·5%.

The determination of liquid scintillation efficiency for intact filter papers permits the entire determination of primary productivity with C^{14} to be performed with one instrument. Absolute activities of available C^{14} (Jitts and Scott, 1961) and fixed C^{14} can be compared readily by using liquid scintillation without encountering any of the problems associated with geiger counting: self-absorption, backscatter, and variable geometry. When liquid scintillation facilities are not available for routine use, the ratio of fixed C^{14} to available C^{14} can be determined accurately by geiger counting only if the geiger efficiency for the samples is known. Precise and accurate determinations of geiger efficiency can be made by liquid scintillation counting of $C^{14}O_2$ recovered from combusted phytoplankton on filter papers. Liquid scintillation counting is also an accurate means of standardizing activities of solutions, such as the $NaHC^{14}O_3$ used for productivity measurements. These two determinations make possible the calculation of primary productivity from absolute measurements of C^{14} with only occasional use of scintillation counting, because instrumental variation in geiger counting can be compensated with a permanent reference standard after the geiger efficiency is determined.

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[1] Filters were dissolved in a scintillation vial containing 5 ml dimethyl formamide, then diluted with 10 ml phosphor solution and counted.

Summary

1. The absolute activities of C^{14}-phytoplankton (collected on filter papers in studies of primary productivity) were determined by liquid scintillation counting of $C^{14}O_2$ recovered after ignition of the sample in an oxygen combustion flask.

2. The efficiency of counting C^{14}-phytoplankton on filter papers with a thin-window gas-flow geiger counter was $25{\cdot}8\% \pm 1{\cdot}19$ (SD).

3. Intact filter papers containing C^{14}-phytoplankton were counted by liquid scintillation with an efficiency approximating that for soluble C^{14}-toluene added as an internal standard.

4. Liquid scintillation appears to be a convenient and reliable substitute for geiger counting in productivity studies.

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INFECTION OF THE WALLEYE, *STIZOSTEDION V. VITREUM*, OF WESTERN LAKE ERIE WITH *BOTHRIOCEPHALUS CUSPIDATUS* (COOPER)

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Introduction

In recent years appreciable changes have taken place in the biota and physicochemical conditions in Lake Erie (Beeton 1961). The accelerated eutrophication of the lake has been accompanied by the near disappearance of several fish species, e.g., blue pike (*Stizostedion vitreum glaucum*), lake herring (*Coregonus artedi*), lake trout (*Salvelinus namaycush*), sauger (*Stizostedion canadense*), and whitefish (*Coregonus clupeaformis*). Interest in the biology of the remaining species has increased as means have been sought to preserve their numbers in the lake. This report, which describes the caecal and intestinal parasites of the walleye, *Stizostedion vitreum vitreum*, is a contribution to the natural history of this fish in western Lake Erie. This study concerns: the type and degree of intestinal parasitic infestations in a single year class of walleyes during their first 3 years of life; seasonal changes in the incidence and maturity of the dominant parasite *Bothriocephalus cuspidatus*; and the effects of the infestations on the physical condition of the host.

Previous parasitological investigations of the walleye in Lake Erie have been few and of limited scope. Hunter and Bangham (1933) reported on new Cestoda and Nematoda from 58 walleyes collected in eastern and western Lake Erie in 1927-29. Bangham[1] described the internal parasites of 26 adult and 12 young walleyes taken from three areas of Lake Erie in 1927 and 1928 (some of these fish may have been included in Hunter and Bangham's 1933 report).

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[1] R. V. Bangham, Summary of Results of Study of Parasites of Lake Erie Fish. Mimeo. 6 pp., undated.

In both of these studies, the cestode, *B. cuspidatus,* was by far the most abundant parasite.

B. cuspidatus has been found in various species of freshwater fish. Cooper (1918) reported it in the goldeye (*Hiodon alosoides*), log perch (*Percina caprodes*), mooneye (*Hiodon tergisus*), sauger, walleye, and yellow perch (*Perca flavescens*). Bangham (see footnote 1) described the infestation of blue pike with *B. cuspidatus,* and Meyer (1954) discovered this parasite in the burbot, *Lota lota.*

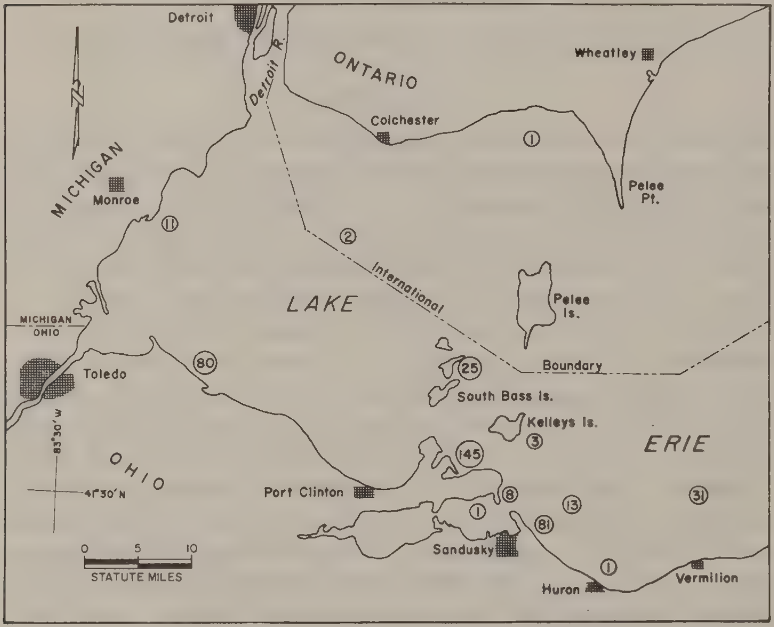
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FIG. 1. Western Lake Erie showing locations (circles) where walleyes were collected. The number of fish taken at each location is indicated within the circle.

Bangham (1948) stated that, although *B. cuspidatus* infected various species of fish, sexually mature parasites appeared to be restricted to members of the pike-perch group—the walleye, blue pike, and sauger. Cooper (1918) found a specimen taken from a logperch "mature but of small size." Van Cleave and Mueller (1934) noted, however, that Cooper's record of *B. cuspidatus* in log perch could have been *B. formosus.*

Of the walleyes that we examined, nearly 50% were infested with caecal and intestinal parasitic worms; of these parasites, 99% were *B. cuspidatus.*

MATERIALS AND METHODS

This study is based on 402 walleyes of the 1962 year class collected during 1962-64—325 young-of-the-year (age-group 0), 58 yearlings (age-group I), and 19 2-year-olds (age-group II)—from 13 locations in western Lake Erie (Fig. 1). Of the total, 14% were taken with commercial trap nets and 86% with trawls fished from the U.S. Bureau of Commercial Fisheries research vessel *Musky II.* The ages of all yearling and 2-year-old fish were verified by examination of their scales.

All young-of-the-year walleyes were preserved whole in 20% formalin after an incision had been made in the abdomen. The viscera of 23 yearlings were removed from freshly caught fish and preserved in 20% formalin. The remaining 35 yearlings were examined when fresh; the parasites were fixed in Bóuin's solution and later transferred to 70% alcohol. The 2-year-old fish were examined soon after capture; the parasites were fixed in alcohol-formaldehyde-acetic acid solution (AFA) and then transferred to 70% alcohol. All examinations of viscera were macroscopic. All parasites were stained in Semichon's acetocarmine and mounted.

BOTHRIOCEPHALUS CUSPIDATUS

Our observations of *B. cuspidatus* from walleyes of western Lake Erie conform very closely with the description given by Cooper (1918), except that he found specimens up to 180 mm long, whereas the largest we collected measured 60.7 mm. We detected some variation in the shape of the scolex (Fig. 2) that was not mentioned in Cooper's description.

According to Essex (1928) the coracidium is fully formed in the egg after an incubation period of 4 to 8 days. Upon release from the egg, the free-swimming coracidium is ingested by a species of *Cyclops.* Essex found *C. brevispinosus, C. bicuspidatus, C. prasinus, C. leuckarti,* and *C. serrulatus* to serve equally well as first intermediate host. Of these copepods, the first four have been found in western Lake Erie (Chandler 1940). The tapeworm larvae moved to the body cavity of the *Cyclops* within 3 hours following exposure; development of the procercoid was considered to be complete in 9 or 10 days, when the cercomer was lost.

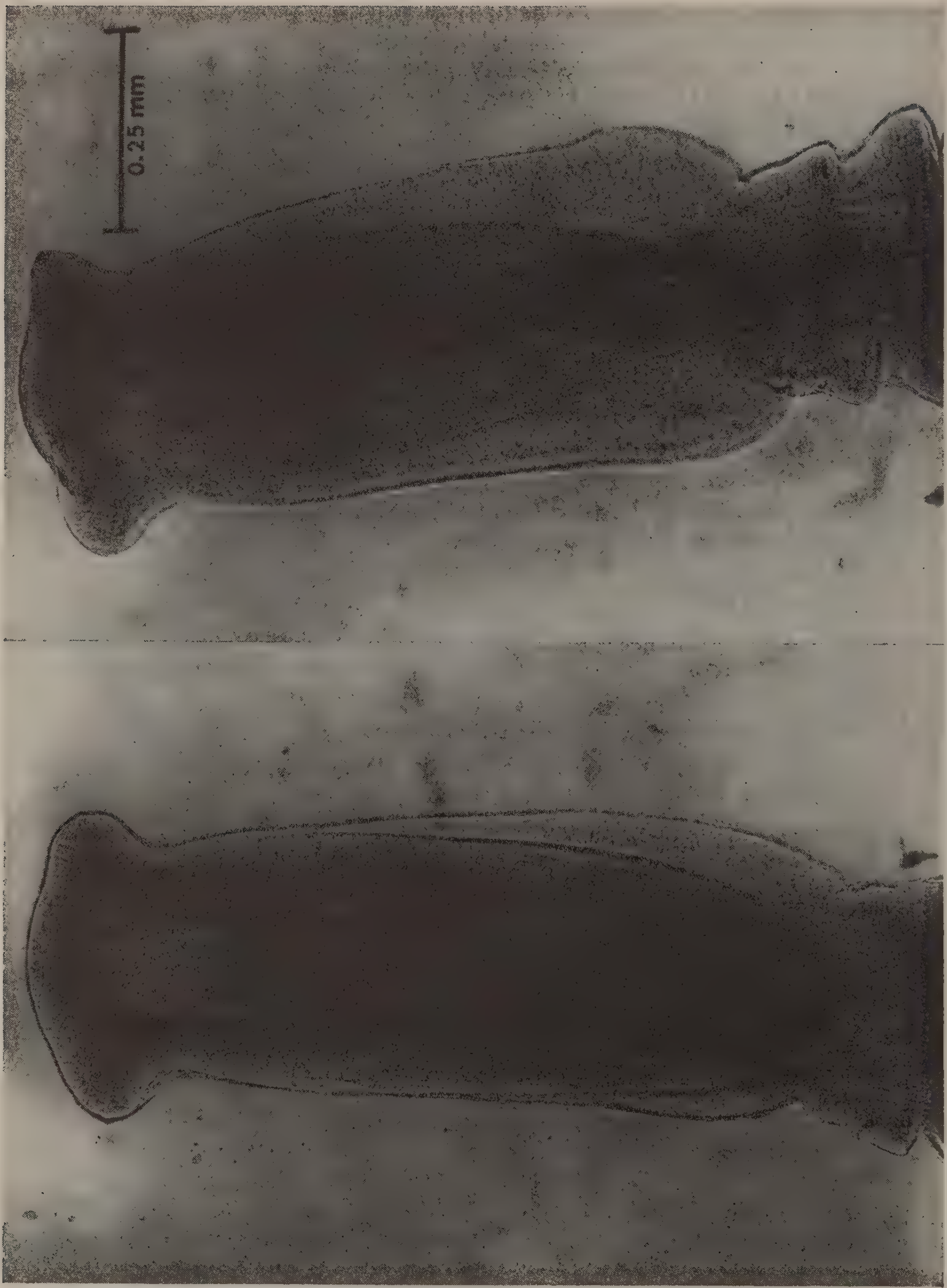

FIG. 2. Photomicrographs of *Bothriocephalus cuspidatus* showing variation in outline of the scolices.

Essex (1928) believed it very unlikely that a second intermediate host was involved, since he found no structures to indicate capability of migration through the intestinal walls to the body cavity of a fish. He suggested that small specimens of *B. cuspidatus* in adult walleyes probably get there either through ingestion of small fish that had recently eaten infected *Cyclops* and digestion of the small fish liberated the copepods, or that the *Cyclops* were strained directly from the water and ingested by the large walleyes.

Increase in incidence with age of host.—Infestation of walleyes of the 1962 year class with *B. cuspidatus* was first noticed in a collection of 106 fish made August 7, 1962 (Table I). The fish were approximately 2½ months old and their average total length was 14.0 cm. 4 walleyes (3.8%) contained *B. cuspidatus*. The incidence increased progressively in collections of young-of-the-year fish during the remainder of the year. The rate of infestation was almost 70% in September and 100% in November (Table I). All but 2 walleyes of this year class that were examined in 1963 and 1964 were infested with *B. cuspidatus*. The only parasite-free yearling walleyes were 2 fish collected on September 20, 1963.

Bangham (footnote 1), who examined 22 adult walleyes from the open lake near Sandusky, Ohio in 1927-28 found that all had larval and adult *B. cuspidatus* in the intestine and pyloric caeca. He also examined 12 young fish from the extreme western end of the lake, of which 5 were parasitized by *B. cuspidatus*. Van Cleave and Mueller (1934) reported that during the summer in Oneida Lake, New York nearly all walleyes were infested with this parasite. Because the ages of the fish examined by Bangham and by Van Cleave and Mueller were not determined, direct comparisons with our findings cannot be made.

Continuing recruitment of tapeworms was evident among the yearling and 2-year-old fish. Since the largest tapeworm in our young-of-the-year walleyes was 23 mm long, we used this length to separate recent from old infestations; specimens less than 23 mm were considered to be of recent origin. Of 20 gravid tapeworms picked at random from among those found in the yearlings, 9 (45%) were less than 23 mm long. In a random selection of 70 gravid worms from 2-year-old fish, 22 (31.4%) were less than 23 mm long. The higher percentages of gravid tapeworms were among fish captured in the late summer (August-September 1962) and spring (May 1963) and lowest in the late fall (Table I). This seasonal

TABLE I

THE OCCURRENCE OF *Bothriocephalus cuspidatus* IN WALLEYES OF THE 1962 YEAR CLASS COLLECTED AT VARIOUS LIFE STAGES

Life Stage and Date of Capture	Number of Fish	Average Fish Length (cm)	Percentage of Fish Infested	Parasites per Infested Fish		Percentage of Gravid Parasites
				Average	Range	
Young-of-the-Year						
Aug. 7, 1962	106	14.0	3.8	< 1.0	0–1	50.0
Aug. 14-23, 1962	42	15.7	21.4	1.3	0–3	41.7
Aug. 28-30, 1962	59	18.4	28.8	1.6	0–4	85.7
Sept. 6-26, 1962	52	21.5	69.2	3.9	0–16	66.7
Oct. 10-18, 1962	54	23.0	77.8	4.5	0–19	33.5
Nov. 1-30, 1962	12	24.4	100.0	9.3	1–21	8.1
	325					
Yearlings						
May 7-21, 1963	23	24.2	100.0	11.1	1–38	70.7
Sept. 20, 1963	12	34.3	83.3	17.8	0–42	34.3
Oct. 30, 1963	23	36.2	100.0	18.0	1–21	0.0
	58					
Two-year-olds						
May 4-5, 1964	19	39.5	100.0	33.9	7–94	35.0
Total	402					

reproductive cycle agrees with other findings on the cestodes of fish (Connor 1943, Essex 1928, Meggitt 1914).

Increase in intensity of infestation with age of host.—The intensity of infestation by *B. cuspidatus* was measured as average number of worms per infested fish (Table I). Young-of-the-year walleyes collected on August 7, 1962 (approximately 2½ months old) averaged less than one tapeworm per fish (range: 0–1). The intensity of infestation increased steadily among the young-of-the-year during the summer and fall of 1962, and by November the average was 9.3 parasites per fish (range: 1–21).

The intensity of parasitization continued to increase during 1963. The average number of worms in the walleyes when first captured as yearlings in the period May 7-21, 1963 was 11.1 per fish (range: 1–38); by October 30, 1963 the average was 18.0 per fish (range: 1–21). The number continued to increase during the winter. Walleyes caught in May 1964 averaged 33.9 tapeworms per fish (range: 7–94). This degree of parasitization is evidently not unusual. Van Cleave and Mueller (1934) reported that the walleyes in Oneida Lake frequently had between 40 and 50 *B. cuspidatus* per fish.

The length of mature tapeworms increased with the increase in intensity of infestation in older fish. The average length of 4 tapeworms in young-of-the-year fish taken in October 1962 was 14.5 mm (range: 8.9–23.0 mm); 20 specimens in yearling walleyes in May-October 1963 averaged 24.8 mm (range: 10.3–57.5 mm); 70 mature tapeworms in 2-year-old fish taken in May 1964 averaged 30.1 mm (range: 9.5–60.7 mm). The largest specimen, 60.7 mm long, was in a fish 41.0 cm long. A large tapeworm (180 mm) found by Cooper (1918) was very likely from a fish much larger than any in our collections.

Effect on host.—*B. cuspidatus* was primarily in the pyloric caeca of the walleyes and was rarely in the stomach or forepart of the intestine. Large parasite burdens (as many as 94 cestodes in one fish) caused the caeca to become greatly distended, but no inflammation was noticed in the caecal tissues. This absence of inflammation might be expected because the unarmed scolices were attached very weakly to the mucosa of the caecal wall.

Since the intensity of parasitism by *B. cuspidatus* increased with the age of the walleyes, possible effects of the infestations on the physical condition of the host were explored. The fish in each collection were divided into two groups on the basis of the mean infestation in that particular sample, i.e., fish with more than the average number of worms and fish with less than the average (Table I). The length-weight relation was calculated separately from measurements of 313 walleyes with less than the mean number of *B. cuspidatus*, and 66 with more than the mean number of worms.[2] The general length-weight equation, $W = cL^n$, where W = weight in grams, L = length in centimeters, and c and n are empirically determined constants, was fitted to each group of measurements (Beckman 1948). The curves were obtained from straight lines fitted by least squares to logarithms of mean lengths and weights for 1.0-cm intervals of length.

The logarithmic forms of the length-weight equations are:

Fish with < mean infestation $\log W = -4.97666 + 2.983 \log L$
Fish with > mean infestation $\log W = -5.30442 + 3.127 \log L$

The empirical data for each length interval (including several intervals represented by only one or two fish) and the curves based on the above equations are shown in Fig. 3. Agreement between empirical and calculated weights of both groups was generally good for the smaller fish; differences were greater for the larger size groups, which were represented by few specimens.

The weight of fish with greater than average infestation of parasites increased more rapidly with increasing length than did that of fish with less than average infestations (Fig. 3). The smallest walleyes showed little difference in weight at any given length between the two groups. As the length (and age) increased, the fish with the greater parasite burdens were heavier at any length than those less severely infected.

Obviously, even the greatest infestations of *B. cuspidatus* we found had no detrimental effect upon the weight of the host. Differences in "condition" between the two groups of walleyes, as reflected by differences in "form" and "fatness," unquestionably owe their origin to variations in the feeding success of individual fish. The greater incidence of worms in the "fatter" walleyes must have resulted from a greater degree of exposure to infection, i.e., the more successful a fish was in capturing food, the greater the number of parasitized prey it consumed.

Geographic distribution in Lake Erie.—Infestation by *B. cuspidatus* did not differ among fish taken at different locations in the western end of Lake Erie (these details are not given here). Bangham (see footnote 1) also found that the degree of infestation of walleyes in Lake Erie by this parasite did not differ noticeably among localities in any one area of the lake.

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[2] The 23 walleyes collected on October 30, 1963 were not weighed.

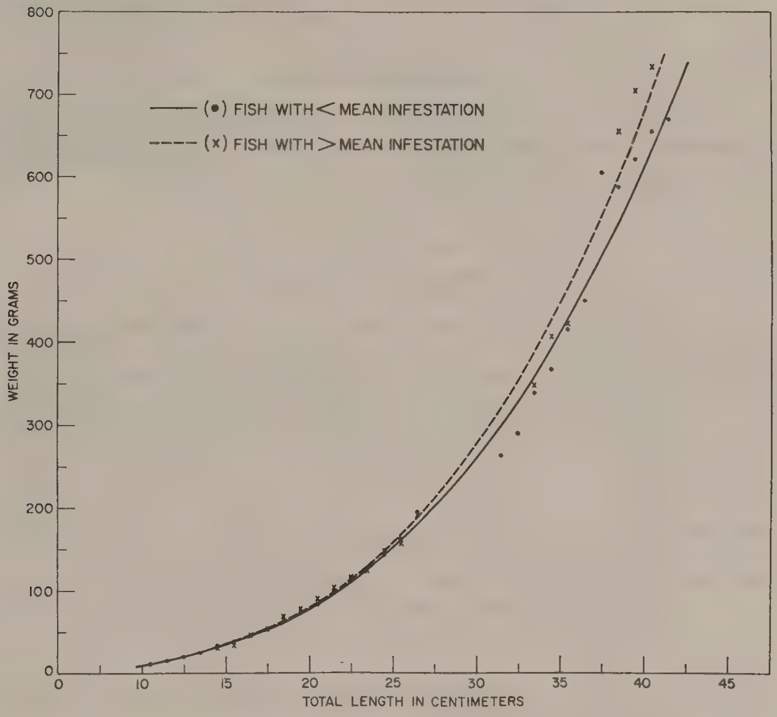

Fig. 3. Length-weight relation of walleyes with more than the mean infestation (broken line) of *Bothriocephalus cuspidatus* and of walleyes with less than average infections (solid line). The crosses and dots indicate the empirical weights for each length interval in each group, respectively.

Other Parasites

We found only 2 other species of parasites in our study: 5 specimens of an unidentified nematode and about 15 specimens of the minute trematode, *Bucephalopsis pusilla.* It was impossible to identify the nematode because of improper preparation. Cooper (1919) found *Bothriocephalus cuspidatus* associated with a cestode of the genus *Proteocephalus,* which Hunter and Bangham (1933) later surmised to be *P. stizostethi.* Hunter and Bangham (1933) found *P. stizostethi* in 13 of 58 walleyes from western Lake Erie. Connor

(1943) also found this species in most walleyes that he examined from Lake Erie. We did not find this parasite. A change in the physicochemical characteristics of the lake (Beeton 1961) may have affected the abundance of either the copepod that is the first intermediate host or the fish species serving as the second intermediate host.

Acknowledgments

Dominic L. DeGiusti of Wayne State University suggested methods of preparing specimens and John G. Hnath, Michigan Department of Conservation, identified the trematode.

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A REVIEW OF PROGRESS IN SURF CLAM RESEARCH

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ABSTRACT

Studies of the biology and of the population dynamics of the surf clam, *Spisula solidissima* Dillwyn, are the two major divisions of the Surf Clam Program at the Bureau of Commercial Fisheries Biological Laboratory, Oxford, Maryland. Advances in our knowledge of the clam have been significant in recent years.

The annual reproductive cycle has been determined for New Jersey clams. Spawning in July is usually followed by a second but minor spawning in the Fall. Sexual maturity appears to be reached at a shell length of about 2-1/2 inches. Growth of juvenile surf clams has been followed at Chincoteague Bay, Virginia, for the past 18 months by sampling a beach population, and by planting and recovering marked clams.

In two 30-day surf clam cruises in 1965, a total of 591 stations were occupied in a 25,000-square-mile area extending from Montauk Point, Long Island, to Cape Hatteras, North Carolina. The number of clams taken, size frequencies, bottom type, associated organisms, temperatures, and salinities were recorded for each station.

Catch data were obtained during 1,400 interviews with boat captains, and 14,000 clams from 785 commercial landings were measured at Point Pleasant, Barnegat, and Cape May-Wildwood, New Jersey, in 1965. The amount of clams discarded at sea by fishermen was observed on individual trips and determined to be of minor importance.

The relation of length to meat-weight was established for each month of 1965 in samples from the fishery. Seasonal changes in clam meat condition, as measured by percentage solids, were also determined in 1965.

A CONTINUOUS-TRANSMISSION, FREQUENCY-MODULATED SONAR FOR THE STUDY OF PELAGIC FISH

by

H.S.H. Yuen

A CONTINUOUS-TRANSMISSION, FREQUENCY-MODULATED SONAR FOR THE STUDY OF PELAGIC FISH

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ABSTRACT

A continuous-transmission, frequency-modulated sonar installed aboard the research vessel Townsend Cromwell of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, operates in two modes: a "search" mode of 52-32 kc for targets up to 1,600 m distant, and a "classify" mode of 290-260 kc for closer examination of nearby targets. On two experimental cruises, effective ranges in the search mode were from 235 m for a single dead skipjack tuna suspended in the water to 800 m for a group of porpoises. The depth distribution of moving subsurface targets showed concentrations in the upper 10 m, at 50-60 m, and at 130-140 m. Species of fish could not be identified with the sonar alone, but fish could be distinguished from porpoises.

INTRODUCTION

The application of sonar to fishery research and commercial fishing has progressed rapidly since World War II. Among the more exciting devices being used for fishery research today are those which combine high resolution and high information rate. Two of these are a sector-scanning sonar (Tucker and Welsby, 1964; Voglis and Cook, 1966) and the continuous-transmission, frequency-modulated (CTFM) sonar. A sonar of the latter type was installed on the research vessel Townsend Cromwell of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, in the spring of 1966. The set was manufactured by Straza Industries[1/], El Cajon, California. It was designed to study the distribution and behavior of tunas and other large, swift pelagic fishes. This report describes the equipment and the preliminary results from our first field tests of it in the vicinity of the Hawaiian Islands.

[1/] Mention of name of firm in this publication does not imply endorsement of its product.

Proc. Indo-Pacific Fish. Coun., 12(II): 258-270.

CHARACTERISTICS OF CTFM SONAR

Principles of operation

The continuous-transmission, frequency-modulated sonar, as its name implies, continuously transmits a signal that changes in frequency, whereas other sonars transmit pulses of sound energy at fixed frequencies. When plotted against time, frequencies projected by the Crowell's sonar form a regular sawtooth pattern. The signal slopes from an upper to a lower frequency, then rapidly returns to the upper frequency for another sweep. A returning echo from a target, e.g. a fish, will also present the same pattern of frequency change, but will lag the projected signal in time. The time lag depends upon the distance between sonar and fish. A comparison of the projected signal and returning echo at any instant of time reveals a frequency difference (Δ f) between the two which is constant for a fixed target distance (Fig. 1). The farther away the fish, the greater will be the time lag and, therefore, the greater the frequency difference.

Generated by a frequency-modulated oscillator, the sawtooth pattern is amplified and then transmitted into the water by the projector (Fig. 2). The echo is received by the hydrophone, amplified in the preamplifier, and compared with the outgoing signal in the mixer. The resulting frequency difference is amplified and then displayed both audibly through a loudspeaker and visually on a cathode ray tube (CRT) after being evaluated in a frequency analyzer. The target appears on the CRT at the bearing the hydrophone is facing.

The sonar operates in two frequency bands (Table I): the "search" mode (52-32 kc) covers ranges up to 1,600 m; the "classify" mode (290-260 kc) provides very high resolution at short ranges. Each mode requires its own hydrophone, projector, and mixer, but since other components are common to both, only one mode can be used at a time.

TABLE I

SELECTED TECHNICAL CAPACITIES OF THE SEARCH AND CLASSIFY MODES OF THE CTFM SONAR ON THE CROMWELL

Characteristics	Search mode	Classify mode
Projected frequencies	52-32 kc	290-260 kc
Projected source levels (referenced to 4μ bar at 1 m)	+100 db	+96 db
Beam shapes		
Projectors	Horizontal 38° Vertical 15°	Conical 15°
Hydrophones	Horizontal 6° Vertical 15°	(1) Horizontal 0.6° Vertical 15° (2) Horizontal 15° Vertical 0.6° (3) Conical 0.6°

Major units

Physically, the sonar is divided into three units: the transducer assembly (Fig. 3) which projects downward from the hull of the ship, the power amplifier console, and the control and display console (Fig. 4). The consoles are located in an air-conditioned electronics room.

The transducer assembly (Fig. 3) consists of a separate projector and hydrophone for each mode. They can be trained horizontally and vertically and lowered and raised. They are retracted into a sea chest when not in use. During operation, the upper transducer is 0.4 m beneath the hull and the lower, 1.5 m. This arrangement places them about 4 m beneath the sea surface.

The power amplifier console houses the amplifiers which drive the projectors and the transducer training motors.

The control and display console (Fig. 4) contains all the remaining electronic components of the system. The system is solid stage and of modular construction.

Operation

The operation of the sonar and the type of data it provides can best be visualized by examining the control and display console (Fig. 5). Illuminated pushbuttons turn the set off and on and select the mode of operation. In the search mode the operator has the choice of five range scales, 100 m, 200 m, 400 m and 1,600 m. The echoes are displayed on the 7-inch-diameter CRT in a plan position indicator display. Thus the center of this display represents the ship's position and the top of the display represents the ship's heading. At each range scale a target must be at least 10 percent of the maximum range from the ship to be detected. Thus in the 100-m range scale, only targets 10 to 100 m away can be detected.

A control stick controls the bearing of the transducer; deflection to the right changes bearing clockwise, to the left counterclockwise. A knob controls the tilt of the transducer from 0° to 90°. Pushbuttons to the right of the CRT select automatic scanning in either bearing or tilt. During automatic scanning the center of the sector is controlled by the control stick and digitally displayed beneath the CRT as "relative bearing". A sector selector is used during automatic scanning in bearing to choose sector sizes of 12°, 45°, 90° or 180° centered at any bearing and tilt. Scan rates are 30° per second at range scales to 400 m, 15° per second on the 800-m range scale, and 7.5° per second on the 1,600-m range scale. Sector size for automatic scanning in tilt is limited to 12°, but the sector can be centered at any tilt and bearing.

The control stick also controls the position of a cursor that appears as a ring of light 5 mm in diameter on the CRT. The position of the cursor is controlled in bearing by manipulating the stick to the right or left, and in range by moving it forward or backward. The position of the cursor is indicated by digital readouts beneath the CRT labeled "cursor range" and "relative bearing". Placing the cursor over a target, the operator reads out the position of the fish relative to the ship.

In the classify mode the operator may either automatically scan a 12° sector in bearing or in tilt with any of the three hydrophone beam shapes indicated in Table I. The display on the CRT is a "B scan". Thus the limits of the display form a rectangle. During horizontal scanning the left and right borders represent the left and right limits of the 12° sector, and the top and bottom borders define a distance equal to one-fifth of the cursor range. During vertical scanning top and bottom borders represent the upper and lower limits of the 12° sector, and the left and right borders define distance. The center of the area being observed is controlled in bearing and range with the control stick and is displayed digitally under the CRT as "cursor range" and "relative bearing".

Other controls allow adjustment of the gain of the audio and the visual displays, correction of the cursor position to account for doppler effects, and shift from active sonar to a passive listening mode.

Outputs lead into a multichannel magnetic tape recorder which has not yet been installed. These outputs were designed to include all information necessary for a detailed playback through the CRT. In addition to the video information, the outputs are led from such controls as range scale, tilt, receiver gain, cursor bearing and range, horizontal or vertical scan, and beam shape (in classify mode).

FIELD TESTS OF CTFM SONAR

From May 28 to June 10 and June 22 to July 20, 1966, the sonar was operated near the Hawaiian Islands to develop searching and tracking techniques and to train sonar operators. Searching was used both day and night to locate targets; tracking was attempted on targets located from the sonar search and from bird flock sightings; and known targets (dead skipjack tuna, *Katsuwonus pelamis*) were examined with the sonar. These experiences provided information on (1) the sonar's effective range, (2) its capability of determining the position of fish and following their detailed movements, and (3) the likelihood that targets can be identified as to family or species from sonar presentations.

Effective range

The effective range was established by using as targets dead skipjack tuna suspended in the water and by locating schools of tuna and other free-swimming animals at sea (Table II, Fig. 6). The maximum distance for which there was a recognizable display on the CRT was recorded. The dead skipjack tuna, 65-75 cm fork length, had an average target strength of -28 db when broadside to a beam of 40 kc (Volberg, Hester and Yuen, MS2/). The ship was allowed to drift away until the dead fish were no longer discernible on the CRT. Maximum ranges on the free-swimming targets were usually obtained when the ship was underway at 3 knots or was stationary.

2/ Volberg, H.W., Hester, H.J., and Yuen, H.S.H. (MS). Acoustic Strength of Several Species of Fish. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

TABLE II

MAXIMUM RANGES AT WHICH VARIOUS ANIMAL TARGETS WERE OBSERVED ON THE CRT DISPLAY

Mode	Target	Maximum range (m)
Search	Dead skipjack tuna (65-75 cm fork length)	
	One	235
	Two (one above other, 30 cm apart)	340
	Three (one above other, 35 cm apart)	380
	Surface skipjack tuna schools (1-11 kg)[1]	650
	School of yellowfin tuna *(Thunnus albacares)* (18 kg)[1]	545
	Subsurface fish (unidentified)	389
	Whitetip shark *(Carcharhinus longimanus)*[1]	340
	Billfish (Istiophoridae)[1]	280
	Porpoise[2] (probably *Stenella attenuata* or *Steno bredanensis*	
	One	ca. 400
	Group	800
Classify	Dead skipjack tuna (65-75 cm fork length)	
	One	130
	Two (one above other, 30 cm apart)	130
	Three (one above other, 35 cm apart)	130

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[1] Identified visually at the sea surface.

[2] Identified from the display of their own sounds on the CRT.

The maximum range at which a single skipjack tuna was observed was 235 m in the search mode and 130 m in the classify mode (Table II). In the search mode this range was extended as the number of skipjack tuna was increased from one to three. The amount of increase was 105 m for the second fish and an additional 40 m for the third fish. Further additions of fish would be expected to increase the range even more, but each new fish presumable would have a progressively smaller effect. In the classify mode the range was not extended as the number of fish was increased, an apparent consequence of the very high resolution in this mode.

Although free-swimming skipjack tuna schools could be detected at ranges as great as 650 m (Table II), maximum sonar range varied considerably among schools (Fig. 6). It was between 200 and 400 m for about 50 percent of the 60 skipjack tuna schools located from bird flock sightings. Six schools that were visible at the sea surface could not be contacted with the sonar. These variations in effectiveness appeared to result primarily from differences in the size of the fish and the height of the sea. The six schools with which no sonar contact was established were composed of fish weighing 1-4 kg and were encountered in seas 1-1.5 m high; during most other contacts the seas were lower and fish sizes ranged up to 11 kg. Fish size and sea state would be expected to have significant effects on the maximum range. Target strengths are much lower for smaller fish (Midttun and Hoff, 1962; Cushing, 1964), and more air bubbles are mixed in the water at the higher sea states. These bubbles not only reflect echoes that tend to mask the echoes from the fish, but also disperse the energy of the signal so that the fish echoes themselves are weakened.

The maximum range achieved by the sonar on animal targets was 800 m, on a group of porpoises (Table II). Porpoise sounds could be heard on the audio presentation and seen on the CRT, on both the active sonar and the listen modes of operation. Consequently they could be located passively in bearing before they could be located actively in bearing and range. Targets of suitable strength, such as the bottom, were perceived up to 1,600 m.

Position and movement of targets

The position of a biological target relative to the ship was established by maneuvering the cursor over the target and adjusting the tilt so that presentation on the CRT reached its greatest intensity. This result was accomplished by switching back and forth from scanning in bearing and in tilt. The range, bearing, and tilt to the target were recorded and used to determine target depth and the horizontal range to the target. These data, recorded at 30-second intervals, established the consecutive positions of the target relative to the ship. The true movement of the target was obtained by reconstructing the ship's path from concurrent data on speed and compass bearing, and then plotting the target positions from the appropriate ship's position. This procedure was used successfully to determine the depth and movement of biological targets.

Some of the most interesting information from the two experimental cruises resulted from the fact that depth could be readily established. As many as 46 unidentified fish targets were located in 13 daylight hours by the use of routine search patterns designed to cover the upper 400 m of ocean. There was no surface indication of their presence. Most of the targets were in the upper 10 m, but a second concentration was located at 50-60 m and a third at 130-140 m. The location of these concentrations can be readily compared with vertical distribution of temperature and salinity. The upper two modes were in the mixed layer (26.5°C) and the deepest mode was in the thermocline at 21.5°C.

On other occasions a skipjack tuna school that had been identified at the surface, was tracked to a depth of 40 m; targets in a mixed group of skipjack and yellowfin tunas were tracked to a depth of 140 m; a whitetip shark was located swimming at 50 m and tracked to the surface, where it was identified; and a porpoise, identified by the sounds it produced, was located at a depth of 230 m and tracked as it swam rapidly to the surface.

Determination of the swimming speed of sonar targets was moderately successful. Repeated contacts at 30-second intervals with targets located during routine search of the upper 400 m made it possible to calculate speeds. These ranged from 0 to 4 knots for different targets. Cruising speed of the whitetip shark was about 2 knots, and that of porpoises around the ship at night ranged from less than 1 knot to about 4 knots.

Attempts to obtain enough consecutive fixes on fish targets to measure long-term persistence of movement were only partially successful. The duration of continuous sonar contact with skipjack tuna schools near the surface ranged from momentary to no more than 18 minutes on all but two occasions. Contact was maintained for 56 minutes with one school of large skipjack tuna and for 3 hours and 39 minutes with a mixed group of skipjack and yellowfin tunas. During each of the two extended periods of contact the ship was stopped and the fish remained within sonar range. The longest continuous contact with an unidentified target at greater depth was 42 minutes. I believe, however, that further experience will show that deeper targets are easier to track for long period than schools near the surface.

Termination of sonar contact with surface skipjack tuna schools was usually caused by the masking of fish echoes from the sea surface (surface reverberation) or by a slow fading of echoes with no increase in target distance. The feature of fading is characteristic of echoes from masses of minute air bubbles in the water. Fellow workers have observed that skipjack tuna breaking the surface always create pockets of air bubbles. I suspect that the departure of the fish is masked by these pockets of air bubbles, particularly because the target strength of skipjack tuna depends upon the aspect of the fish relative to the sound beam (Volberg, Hester, and Yuen, MS, see footnote 2), and skipjack tuna are known to make sudden maneuvers while feeding at the surface (Strasburg and Yuen, 1960).

Species identification

Target identification has been a major concern among those who use sonars. If biological targets could be identified to species from echoes alone, the sonar would be an even more powerful tool than it now is, especially in the assessment of oceanic populations. Although success in identifying targets during these first two cruises was limited, the sonar encounters with an assortment of species of various sizes led me to the opinion that species identification will ultimately be possible.

Porpoises already can be distinguished from fish because their sounds are clearly discernible on the sonar. The various fish species cannot yet be distinguished by their sonar presentation, but many variations have been observed. Targets differ greatly in strength, shape, size, grouping, speed of travel, and depth beneath the sea surface. These and other characteristics can be quantified and applied to target identification.

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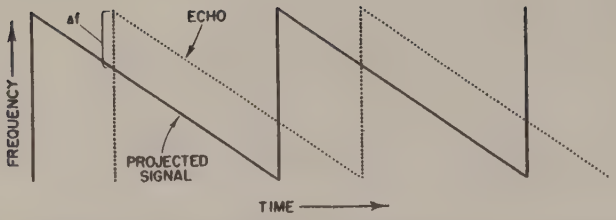


Fig. 1. Frequency Difference (Δ f) Between Projected Signal and Echo of CTFM Sonar

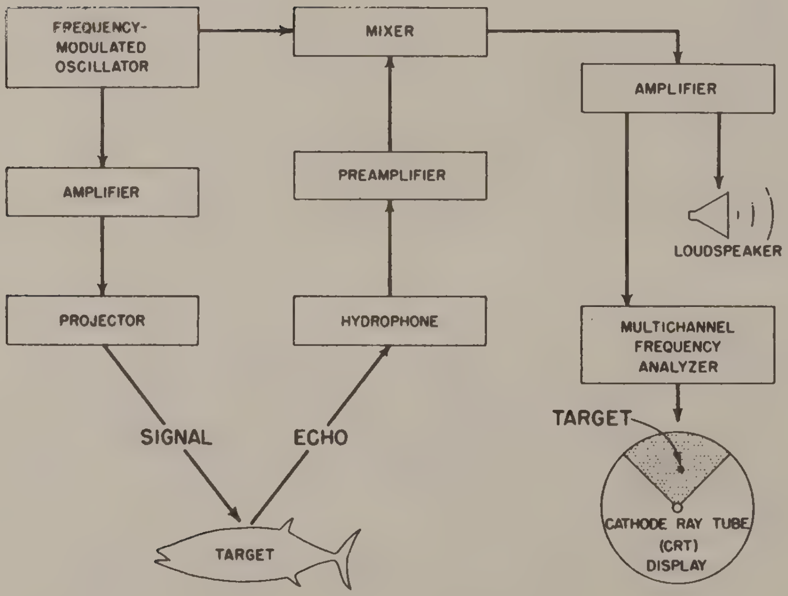

FREQUENCY-MODULATED OSCILLATOR
MIXER
AMPLIFIER
AMPLIFIER
PREAMPLIFIER
LOUDSPEAKER
PROJECTOR
HYDROPHONE
MULTICHANNEL FREQUENCY ANALYZER
SIGNAL
ECHO
TARGET
TARGET
CATHODE RAY TUBE (CRT) DISPLAY

Fig. 2. Simplified Block Diagram of CTFM Sonar System.

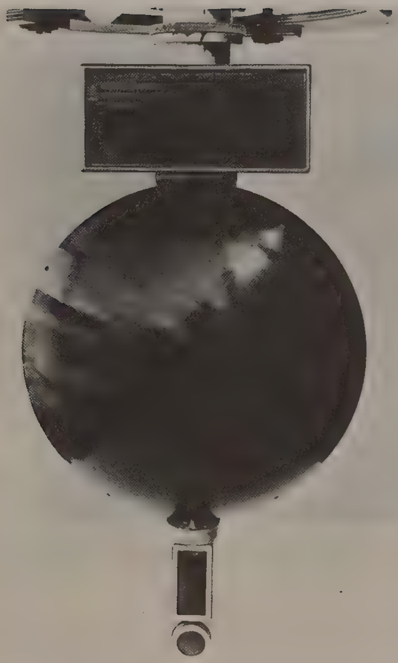


Fig. 3. Transducers of CTFM Sonar on Townsend Cromwell. Top Rectangle is Search Hydrophone; Large Circle is Protective Dome of Classify Hydrophone; Bottom Piece Includes the Search and Classify Projectors

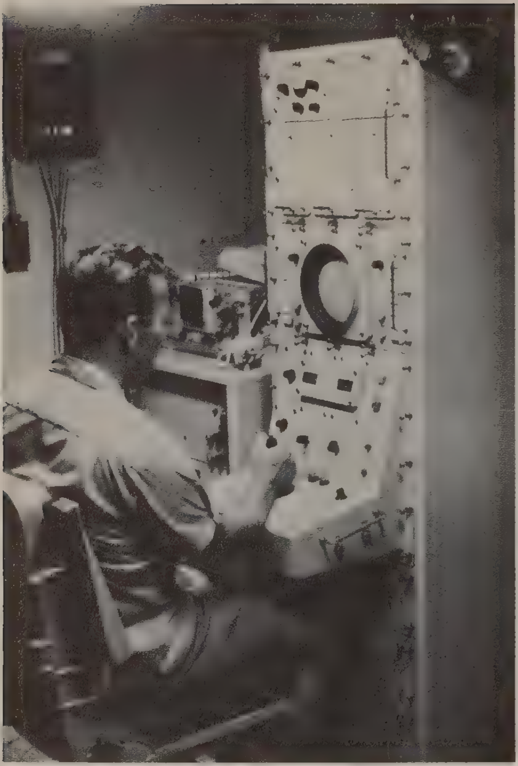
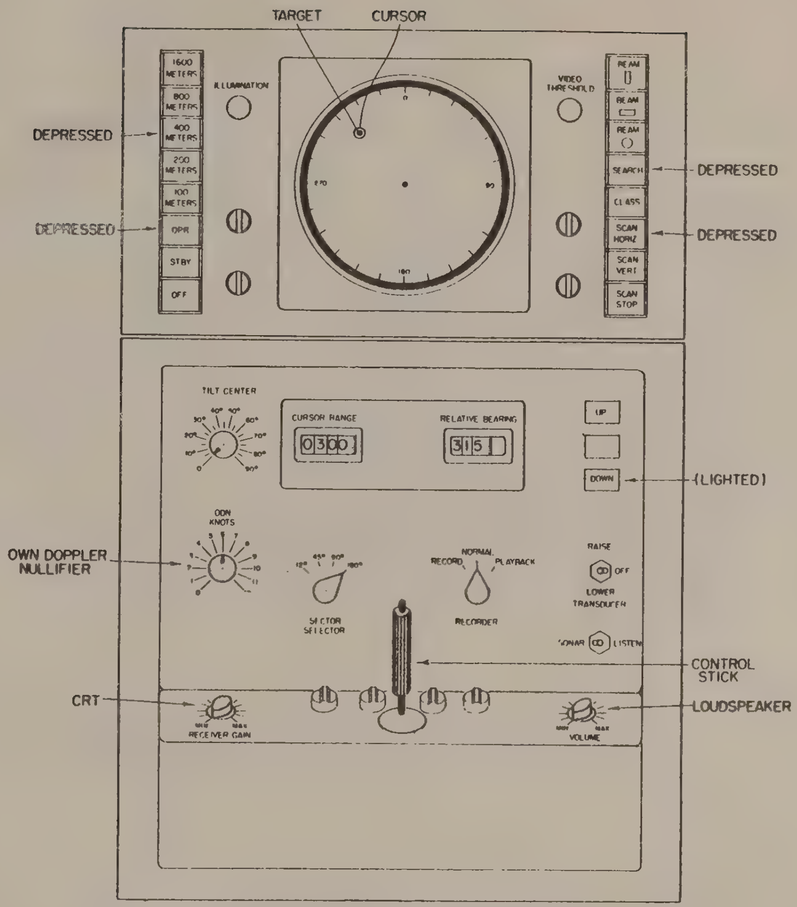


Fig. 4. Control and Display Console of CTFM Sonar


TARGET
CURSOR
DEPRESSED
DEPRESSED
1600 METERS
800 METERS
400 METERS
200 METERS
100 METERS
OPR
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OFF
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90
180
270
VIDEO THRESHOLD
BEAM
BEAM
BEAM
SEARCH
CLASS
SCAN HORIZ
SCAN VERT
SCAN STOP
DEPRESSED
DEPRESSED
TILT CENTER
CURSOR RANGE
0300
RELATIVE BEARING
315
UP
DOWN
(LIGHTED)
OWN DOPPLER NULLIFIER
ODN KNOTS
SECTOR SELECTOR
NORMAL
RECORD
PLAYBACK
RECORDER
RAISE
OFF
LOWER TRANSDUCER
SONAR
LISTEN
CONTROL STICK
CRT
MIN
MAX
RECEIVER GAIN
LOUDSPEAKER
MIN
MAX
VOLUME

Fig. 5. Control and Display Panel of the CTFM Sonar. In this Drawing, the Sonar is Being Operated in the Search Mode and is Scanning Horizontally within a 400-m Range. On the CRT the Target is Centered within the Illuminated Ring that Serves as a Cursor. The Target (Note "Cursor Range") is at 300 m; its Bearing ("Relative Bearing") from the Ship is 315°

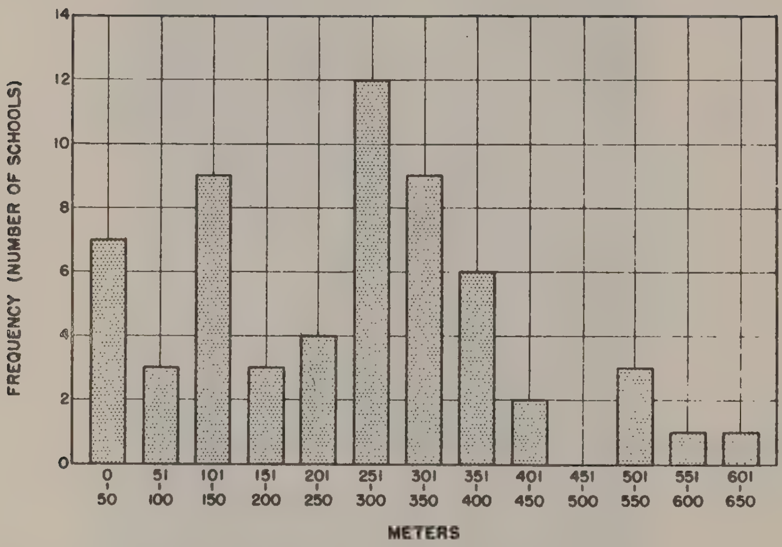

Fig. 6. Frequency Distribution of Maximum Range of Sonar Contact with Schools of Skipjack Tuna

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